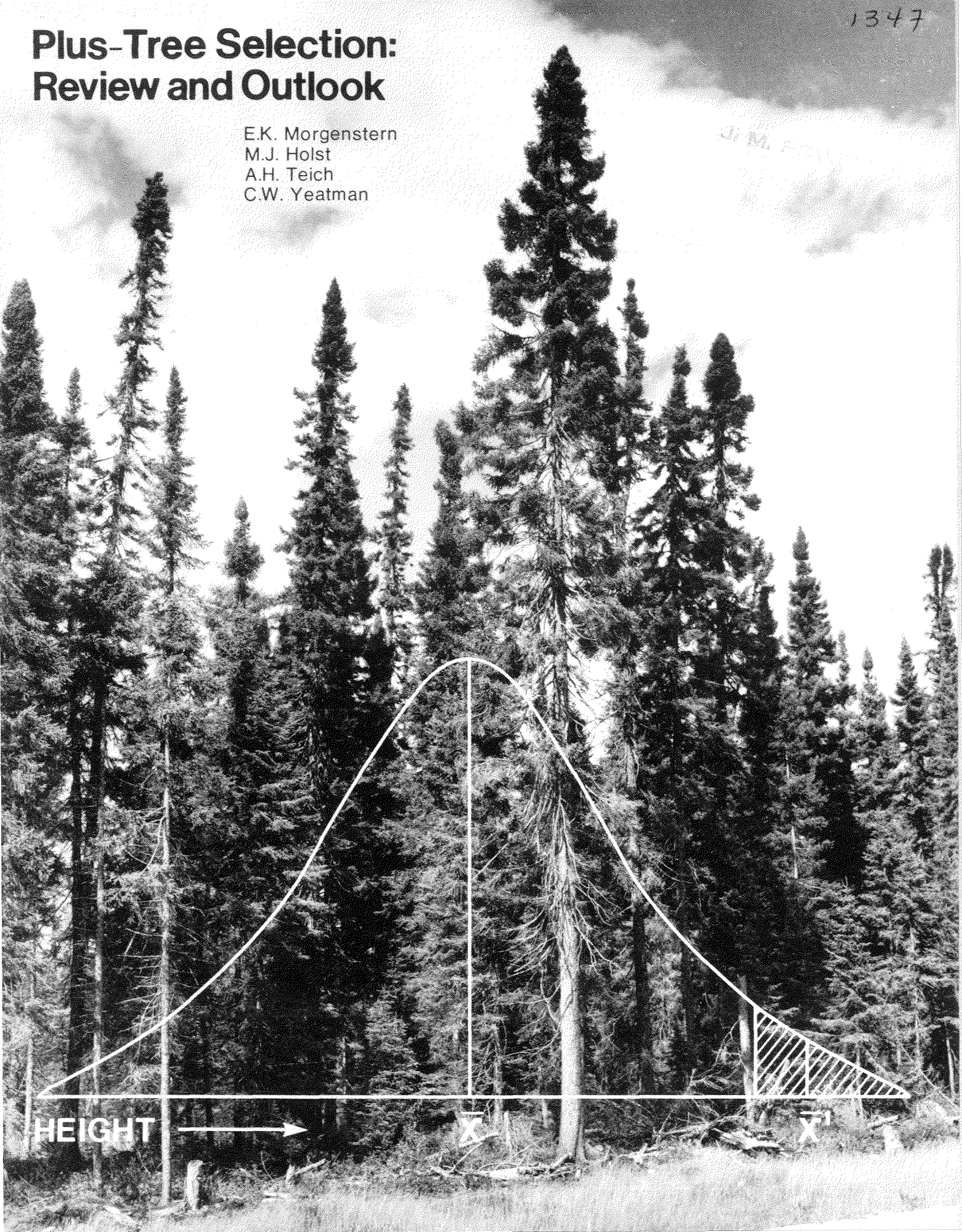


# Plus-Tree Selection: Review and Outlook

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# PLUS-TREE SELECTION: REVIEW AND OUTLOOK

by

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## ABSTRACT

Plus-tree selection has been applied in different parts of the world to artificially regenerated forests for about 25 years. For the benefit of management foresters and specialists cooperating in a selection program, a review is presented of the genetic concepts, breeding methods, and considerations involved in an integrated program plan. It is emphasized, first, that the efficiency of a selection program depends upon the genetic information available for the species and the populations examined and, second, that a program must be built upon a broad genetic base, with many genotypes, to make it flexible in the face of changing silvicultural practices, utilization of new products, and the introduction of new insects and diseases.

An outlook for plus-tree selection in white spruce (*Picea glauca* [Moench] Voss), black spruce (*P. mariana* [Mill.] B.S.P.), red pine (*Pinus resinosa* Ait.), and jack pine (*P. banksiana* Lamb.) illustrates the different approaches required in species that differ in ecology, silviculture, and utilization of wood products.

## RÉSUMÉ

Depuis environ 25 ans, la sélection des arbres plus est appliquée dans différents pays du monde aux forêts régénérées artificiellement. Pour le bénéfice des aménagistes forestiers et des spécialistes qui coopèrent à un programme de sélection, les auteurs passent en revue les concepts génétiques, les méthodes d'hybridation et certains aspects concernant un plan de programme intégré. En *premier* lieu, ils insistent sur le fait que l'efficacité d'un programme de sélection dépend des informations génétiques disponibles sur telle espèce et sur les populations examinées; en *second* lieu, le programme doit être fondé sur une large base génétique, avec plusieurs génotypes, afin qu'il devienne flexible devant la pratique changeante de la sylviculture, l'utilisation de nouveaux produits et l'introduction de nouveaux insectes et de nouvelles maladies.

Une vue d'ensemble sur la sélection des arbres plus d'Épinette blanche (*Picea glauca* [Moench] Voss), d'Épinette noire (*P. mariana* [Mill.] B.S.P.), de Pin rouge (*Pinus resinosa* Ait.) et de Pin gris (*P. banksiana* Lamb.) illustre les différents façons d'aborder le problème chez des espèces dont l'écologie, la sylviculture et l'utilisation des produits du bois sont différentes.



## PREFACE

In recent years silviculture has been intensified in Canada to increase social and economic benefits from future forests. At least 300,000 acres of forest land are regenerated annually by planting and seedling, and site preparation, seed and planting stock, and tree establishment and maintenance represent a substantial investment. If good returns are to be obtained from this investment, it is vital that the best plant material be used, i.e. trees that are vigorous and healthy, respond well to management, and produce high-quality raw material in a short time. Such trees can be obtained by breeding new populations from those now existing in wild forests. Of several methods available, the selection of "superior" or "plus" trees has received the greatest attention and is most widely employed.

A plus-tree selection program requires the coordinated efforts of scientists and practitioners and good planning based on the utilization of the latest research results. The development of a program is therefore a challenging task. Such development can be assisted by:

1. Explaining the genetic principles of selection to management foresters and those engaged in silvicultural planning and research in related disciplines. Effective communication between specialists will be most easily established if the basic theory is well understood.
2. Reviewing the experience acquired elsewhere. Selection programs have been under way in several areas (Scandinavia, the southern United States) for some time, and a review of these advanced programs will help us avoid poorly planned and narrowly based selection programs that will prove ineffectual in the long run.
3. Discussing the application of genetic theory and selection principles to a number of commercially important species in eastern Canada.

The objective of this report is twofold: firstly, to present a review of the principles of plus-tree selection and, secondly, to discuss ways of applying these principles to white spruce, black spruce, red pine, and jack pine. Although genetic information on these species has only been obtained for the relatively short period of 20 years, the conclusions reached will assist those who are at present developing selection programs.

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# REVIEW OF THE PRINCIPLES OF PLUS-TREE SELECTION

by

E.K. Morgenstern

## INTRODUCTION

Plus-tree selection has been pursued consistently only during the last 25 years. As a general introduction to the subject, many individual descriptions are available that contain little complicated theory but are well illustrated, such as the papers of Bouvarel (1955), Rudolf (1956), Ontario Department of Lands and Forests (1963), Dawson and Read (1964), Clausen and Godman (1967), Georgia Forestry Commission (1967), and Stephenson and Snyder (1969).

In this review the intention is to discuss theory more broadly and to summarize the principles that have been developed. It is obvious that plus-tree selection involves the application of genetic principles, but even the first step, the selection of trees in the forest, will be carried out most effectively if a general plan of the program exists. Consequently, this review consists of three parts - (1) genetic concepts, (2) breeding methods, and (3) the integration of theory in program development. It is not possible to treat each part exhaustively and to cite all of the relevant literature, but the intention is to deal with the main problems arising in breeding programs that utilize plus trees as starting points. A glossary at the end defines certain terms used in the text.

## GENETIC CONCEPTS

### Genes, Genotypes, Populations, Gene Pool

The genes, i.e. hereditary factors, are carried in the chromosomes of an organism and collectively determine its genotype. A normal diploid organism derives one set of chromosomes from its female parent and another, complementary, set from its male parent. Genes appear in different forms at a given chromosome position; these are called gene alleles. In the simplest situation, with two alleles, one allele is contributed by the female parent and the other by the male parent. Many genotypes grouped together in space and exchanging genes by cross-fertilization constitute a population. By acting on populations in different ways, the genetic processes of mutation, natural selection, migration, and random genetic drift give rise to differences in gene frequencies among populations. All gene alleles in a population constitute the gene pool, i.e. the material available to the breeder (Lerner 1958; Sinnott et al. 1958).

## Qualitative and Quantitative Traits

Gregor Mendel's experiments with garden peas could be easily analyzed because he considered clear-cut, qualitative traits. The same flower colors - red, white, and pink - could always be distinguished. A few genes with large effects, called major genes, explained inheritance adequately. Simple counts of the number of offspring in each class revealed certain ratios and were sufficient to analyze such inheritance patterns (Crow 1966). Evidence for the presence of simple Mendelian ratios was also found in the leaf color and branch habit of the Siberian pea shrub, *Caragana arborescens* Lam. (Cram 1958), and the male flower color of Scots pine, *Pinus sylvestris* L. (Carlisle and Teich 1970).

In contrast, in plant breeding, the majority of economic traits, such as yields of crops and diameter and height of trees, differ in degree only. These are quantitative traits, the phenotypic expression of which is much influenced by environment and many minor genes, i.e. genes having small effects. Inheritance of this kind must be studied on the basis of measurement of populations and genetic variances (Falconer 1960).

This distinction between the two types of traits just described is useful here as an indication of the need to use more complex methods in breeding than Mendel used in his experiments. Yet the basic laws of gene transmission are the same; quantitative genetics is merely an extension of basic Mendelian principles (Falconer 1960).

Once trees are examined systematically for differences in easily recognizable traits, a great deal of variation is found. An example is a white spruce (*Picea glauca* [Moench] Voss) with extremely narrow branch angle discovered at Petawawa Forest Experiment Station (Fig. 1). Progeny of this tree indicated that branch angle is probably inherited as a quantitative trait.

## Environmental, Phenotypic, and Genetic Variances

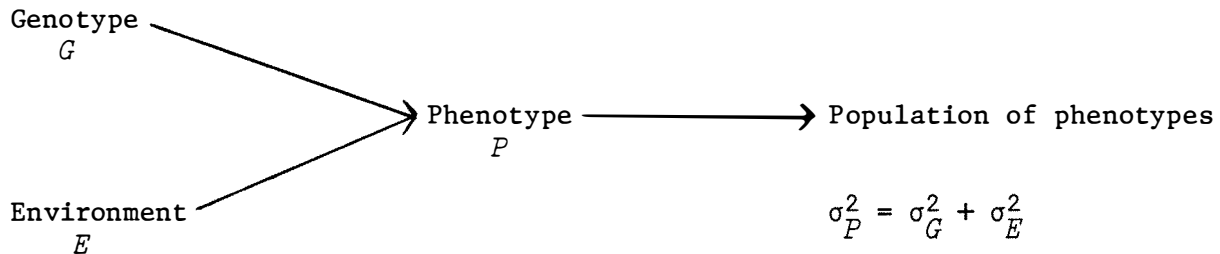
In most forests it is easy to see that trees of a particular species vary in morphological traits, such as form and size; they also vary in other less obvious physiological attributes and in wood qualities, which can only be measured in the laboratory. The appearance of a tree, its phenotype, is determined by both the genotype and the environment; i.e. the interaction of a certain genotype with its environment produces the phenotype, which we observe. In some cases much of the variation may be due to genes and in others to environment. Economically important traits under strong genetic control are of greatest interest to the breeder because they can be most easily changed.

The relative importance of genotype and environment in determining the expression of a trait (i.e. trait heritability) is measured in randomized and replicated experiments, by analysis of variance (Steel and Torrie 1960). The variance is a measure of variation calculated by summing the



*Figure 1. A white spruce with an extremely small branch angle growing at Petawawa Forest Experiment Station. Branch angle is important because of its effect on pulp and lumber quality, and is probably inherited as a quantitative trait.*

squared deviations from the population mean. The application of analysis of variance will be demonstrated in the next section, but it is useful, first, to express the relation of genotype, environment, and phenotype symbolically and in mathematical terms:



The joint effect of genotype and environment produces the phenotype, and a population of phenotypes has a variance resulting from the addition of genetic and environmental variance. The mathematical statement assumes independence of environmental and genetic effects (Le Roy 1966), which can be achieved in an experimental situation by replication and randomization.

To plan a breeding program, it is important to know not only the relative role of genetic variance,  $\sigma_G^2$ , but also its composition. Genetic variance is made up of additive variance and dominance variance, and the relative contribution of each to the inheritance of a given trait is obtained from controlled crosses.

Additive genetic variance means that the progeny of a cross is intermediate in value between the parents (i.e. it is the average of the parents) when environmental effects are absent. The importance of additive variance is that it makes selection predictable, and the ease with which a quantitative trait can be improved depends upon additive variance only. All individuals with high values of a certain trait can be selected.

Dominance genetic variance measures the deviation of progeny performance from the mean of two parents. A large dominance variance in quantitative traits makes selection less predictable than with large additive variance and requires more complicated selection procedures to improve a crop. Specific individuals, which when mated produce high-quality offspring, will have to be found.

### Heritability

The concept of heritability is an important one for the breeder, it being one of the concepts developed to plan a breeding program rationally. Heritability is defined as the "degree to which a character is influenced by heredity as compared to environment" (Snyder 1972) or, in terms of the previous discussion, as the proportion of genetic variance in phenotypic variance. Depending upon the type of genetic variance estimated, different types of heritability may be calculated (see Glossary).

The calculation of heritability will be exemplified by means of data from black spruce, *Picea mariana* (Mill.) B.S.P., growing at Petawawa. Individual 10-year-old seed-bearing trees were located at random in a plantation and their height was measured. Seedlings were raised from these individual trees and tested in 10-tree plots with four replicates on each of two nursery sites. The mean annual height growth of the female parents and their progeny at age 4 is shown in Table 1. Each value given for the progenies is the mean from all four plots at each site.

First, heritability will be calculated by the method of parent-progeny regression. It is easily seen that, if the parental capacity for growth in height is controlled by genes to some extent, this capacity is also transmitted to the progeny. The degree of control is indicated by the regression coefficient (Falconer 1960). We will use the regression of the progeny from Site 1 on the female parents, as shown in Fig. 2, and calculate the following four quantities (Steel and Torrie 1960):

$$\text{Mean height growth of parents, } \bar{x} = 20 \text{ cm} \quad (1)$$

$$\text{Mean height growth of progeny, } \bar{y} = 16 \text{ cm} \quad (2)$$

Sum of the squared deviations of parents from their mean,

$$\Sigma (x - \bar{x})^2 = \Sigma x^2 = 48 \quad (3)$$

TABLE 1. MEAN ANNUAL HEIGHT GROWTH OF SIX BLACK SPRUCE PARENT TREES AND THEIR PROGENIES TESTED AT 4 YEARS OF AGE ON TWO NURSERY SITES

Parent tree no.	Height growth (cm/yr)			
	Parent	Progeny		
		Site 1	Site 2	Progeny totals
1	24	17	14	31
2	19	15	12	27
3	22	17	14	31
4	19	15	13	28
5	21	18	12	30
6	15	14	13	27
Sum	120	96	78	174
Mean	20	16	13	14.5

$$\text{Sum of cross products, } (x - \bar{x})(y - \bar{y}) = \sum xy = 20 \quad (4)$$

The regression coefficient,  $b$ , is determined from the ratio:

$$b = \frac{\sum xy}{\sum x^2} = \frac{20}{48} = 0.42$$

An increase of 1 cm in a parent causes a 0.42 cm increase in the progeny. We may calculate heritability directly from the  $b$  value. According to Falconer (1960), the heritability ( $h^2$ ) based on additive genetic variance is:

$$h^2 = 2b$$

Hence the value of  $b$  obtained above must be multiplied by 2 and

$$h^2 = 0.84$$

Therefore, for the purposes of this discussion (and neglecting problems of statistical significance and precision, e.g. the standard error), it may be stated that 84% of the variation in height growth is of genetic origin.

An estimate of heritability from regression is the easiest to understand but is also, unfortunately, the most problematical. Very few

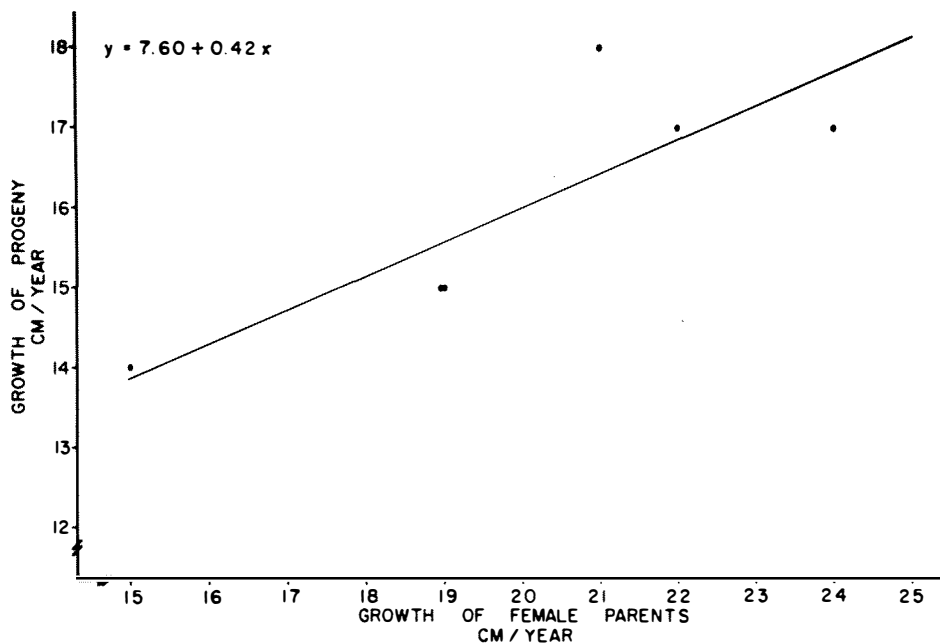


Figure 2. The regression of black spruce mean annual progeny height growth on the mean annual height growth of their female parents.

investigators have found that it gives meaningful results for the growth of forest trees (Steinhoff and Hoff 1971). The following are only three of the problems:

1. The values of  $x$  should be measured without error (Steel and Torrie 1960) or at least on an equal basis, but this is not often the case because the parents grow on different microsites and may be subject to unequal degrees of competition.
2. Identical characters should be measured; yet parental growth during a 10-year period, and progeny growth during a 4-year period, may be correlated, but not necessarily identical, characters.
3. In our example the regression of progeny from only one site on their parents does not permit the exclusion of the progeny-environment interaction.

A more commonly applied technique for the calculation of heritability utilizes only the progeny response, which is subjected to an analysis of variance (Steel and Torrie 1960). For illustrative purposes, the model of analysis chosen is of the simplest kind, and the calculations from figures in Table 1 are as follows:

Site totals: Site 1, 96 cm; Site 2, 78 cm; both sites, 174 cm

Progeny totals: 1, 31 cm; 2, 27 cm; etc....6, 27 cm

Correction factor:  $174^2/12 = 2,523$

Total sums of squares:  $(17^2 + \dots 13^2) - 2,523 = \underline{43}$

Sums of squares for sites:  $(96^2 + 78^2)/6 - 2,523 = \underline{27}$

Sums of squares for progenies:  $(31^2 + \dots 27^2)/2 - 2,523 = \underline{9}$

Sums of squares for interaction progenies x sites:  $43 - 27 - 9 = \underline{7}$

The completed analysis of variance is shown in Table 2.

TABLE 2. ANALYSIS OF VARIANCE OF MEAN ANNUAL HEIGHT GROWTH OF THE SIX PROGENY GROUPS ON TWO NURSERY SITES

Source of variation	Degrees of freedom	Sums of squares	Mean squares	Expected mean squares	Variance components
Sites	1	27	27.00	$\sigma_I^2 + 6\sigma_S^2$	4.27
Progenies	5	9	1.80	$\sigma_I^2 + 2\sigma_F^2$	0.20
Progenies x sites	5	7	1.40	$\sigma_I^2$	1.40
Total	11	43			



The variance components are then obtained by setting calculated mean squares in Table 2 equal to expected mean squares, namely:

$$\text{Interaction, } \sigma_I^2 = \underline{1.40}$$

$$\text{Progenies, } \sigma_F^2 = (1.80 - 1.40)/2 = \underline{0.20}$$

$$\text{Sites, } \sigma_S^2 = (27.00 - 1.40)/6 = \underline{4.27}$$

The component for progenies estimates one-fourth of the additive genetic variance (Falconer 1960). Progenies are considered families of half-sibs (having one parent in common) and therefore designated as  $\sigma_F^2$ . The heritability, here the proportion of additive genetic variance in total phenotypic variance, can then be obtained from:

$$h^2 = \frac{4 \sigma_F^2}{\sigma_F^2 + \sigma_I^2} = \frac{4 (0.20)}{0.20 + 1.40} = 0.50$$

A component for error variance would normally be included in the denominator but is not available in this simplified case. The heritability of mean annual height growth is 50%. In this analysis, it is something like an assessment of the consistency of the response in different environments. A high degree of consistency indicates strong genetic control and, conversely, minor environmental influence. The value obtained is lower than that in the regression estimate from one site, which is as it should be because the progeny-environment interaction has now been accounted for and has been subtracted from the progeny component. Yet the estimate is not of general validity and applies only to the small sample of progenies and environments included in this example.

### Response to Selection

Once heritability estimates have been obtained for a character from an adequate sample of populations and environments, it is possible to predict the response to selection or genetic gain. This is needed to evaluate costs and benefits. Assuming that we are dealing with a quantitative trait in which additive genetic variance predominates, we need to know:

1. The selection differential ( $S$ ). This is the difference between the trait mean of the selected individuals and the trait mean of the unselected population (Fig. 3).
2. The standard deviation of the trait ( $\sigma_P$ ). A parameter of trait variability in phenotypes of the population in which selection is carried out.
3. The intensity of selection ( $i$ ). The proportion of selected individuals, usually expressed by the selection differential ( $S$ ) in standard deviations of the trait  $i = S/\sigma_P$ , obtained from tables for different population sizes.

4. The heritability ( $h^2$ ). In this example, an estimate of the proportion of additive genetic variance in total phenotypic variance; i.e.  $\sigma_A^2/\sigma_P^2$ .

By using the preceding parameters, the genetic gain or response to selection,  $R$ , can then be calculated from the equation

$$R = i\sigma_P h^2$$

When figures are applied from the preceding study of mean annual height growth and it is assumed that only one, i.e. the fastest growing family, is selected,

$$R = 1.267 \times 1.26 \times 0.50$$

$$= 0.80 \text{ cm (or } 0.80/14.5 = 6\% \text{ of the progeny mean)}$$

where  $i = 1.267$ , i.e. a proportion of 1 in 6 = 0.16 (expressed as the standardized selection differential, taken from a table in Becker [1967], p. 111).

$\sigma_P = \sqrt{0.20 + 1.40} = 1.26$ , i.e. the square root of the denominator in the preceding heritability calculation, which represents phenotypic variance, and

$$h^2 = 0.50, \text{ the heritability.}$$

The example shows that the response to selection or genetic gain based upon family means only is 0.80 cm or 6%. This could be increased by selecting the tallest individual within the tallest family. The value for  $R$  is low, but this is not surprising in view of the small population of only six families considered. In this small population the variability was exceptionally low and led to a very small value for  $\sigma_P$ . Any real selection program would be based on a much larger number of families.

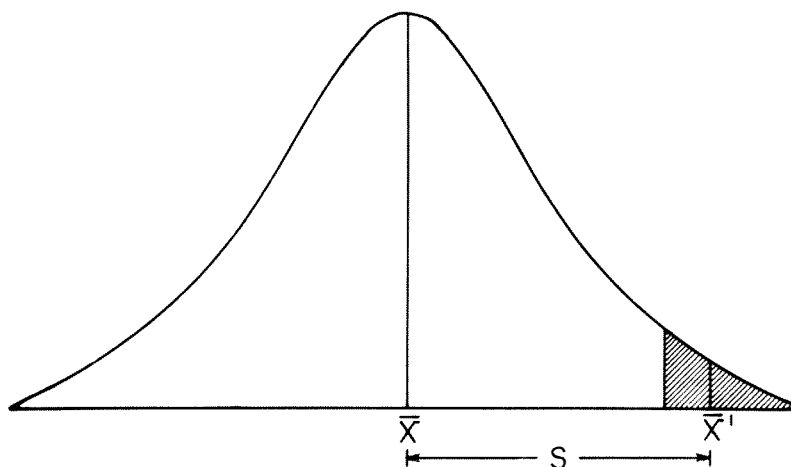


Figure 3. The selection differential,  $S$ . This is the difference between the trait mean in the original, unselected population and the trait mean in the selected group.

## Genetic Correlation and Multiple-trait Selection

The correlation between traits that is directly observed is a phenotypic correlation, since the expression of every trait is influenced by both genotype and environment. When the influence of environment is removed, as in an appropriate analysis of progenies from open-pollinated or control-pollinated parents, and the progenies have been grown in replicated experiments on several sites, the genetic correlation can be obtained (Becker 1967). The origin of genetic correlation is a particular chromosome structure causing pleiotropism or linkage (see Glossary).

The effect of genetic correlation is that, if selection is carried out for one trait, other traits may be simultaneously affected (the exception is zero correlation, i.e. completely independent inheritance of traits). Positive correlation yields additional benefits without extra effort - e.g., if height and diameter are positively correlated. Negative correlation, on the other hand, greatly complicates selection - e.g., if fast height growth is genetically correlated with poor stem form. Even a zero or small genetic correlation complicates selection: if a desired level of improvement for one trait requires a selection intensity of 1%, one tree being selected in 100, selection for two traits requires selection of one tree in 10,000, and selection for three traits the selection of one tree in 1,000,000. The cost of such a program would be prohibitive. With zero or negative correlation, therefore, selection must be limited to very few traits.

A jack pine combining two negative attributes is shown in Fig. 4.

## BREEDING METHODS

### Types of Breeding Methods

In plant crops, several breeding methods are being applied, such as mutation breeding, inbreeding, hybridization, backcross breeding, and selection (Allard 1960). The breeding method or methods used in any particular species depend upon its pollination system (i.e. whether the species is mainly self- or cross-pollinating), the degree of variability, the program goals (i.e. increase in yield or resistance to introduced diseases etc.), and the method of seed production. Selection is the most common method applied in forest trees. It is suitable for the cross-pollination system of many species, and the large variability present in wild species, which are usually hardy and well adapted to their environments. Furthermore, selection is the simplest and most promising method to obtain sizeable genetic gains in the first generation and to meet the demand for large amounts of improved seed (Shelbourne 1969a; van Buijtenen et al. 1971).

### Breeding Methods Based upon Plus-tree Selection

Selection can be carried out among geographic sources (among regions), among stands of the same geographic source (within regions), and



Figure 4. A jack pine with small branch angle and coarse branches observed near Sioux Lookout, Ontario. If the association between branch angle and branch size is consistent, as shown by a substantial negative genetic correlation obtained in experiments, selection against both these negative characters is simplified.

among trees within stands. Only the last two levels of variation will be considered here. The general procedure followed is that good phenotypes are located in natural or planted forests and then reestablished from seed, or by grafting or rooting, in seed orchards. A seed orchard is an artificial population established for the purpose of producing improved seed in quantity. This goal is sought by some or all of the following means (Matthews 1955; Zobel et al. 1958; Johnsson 1964; Dyer 1967):

1. isolation from the surrounding wild population to avoid pollination by outside pollen;
2. selection of a locality favorable with respect to climate, soil, and application of management;
3. promotion of early flowering by grafting of mature scions;
4. avoidance of inbreeding by randomization of clones or genotypes;
5. maximization of seed yield through cultural practices such as fertilization, maintaining wide spacing, bending, or girdling of stems, root pruning, irrigation, and control of weeds, animals, and diseases.

Thus seed production in seed orchards can be advantageous even without genetic gain because production can be enhanced, inbreeding reduced, and seed quality improved over that in natural stands.

#### *Clonal seed orchards without progeny tests*

The method used here consists in tree selection in wild or planted stands, grafting of scions onto rootstocks, and establishment of seed orchards. No progeny-testing is carried out. The method depends upon a sufficiently high heritability of the character considered in selection to obtain some genetic gain (Namkoong et al. 1966) and a high graft compatibility of scion and rootstock within the species (Copes 1967; Karlsson 1970). It offers limited advantages only, particularly if a long-term selection program is expected with selection over several generations, because the best clones will not be identified. It may be a very appropriate method, however, if the natural populations are in danger of being lost or produce little seed in their natural habitats. The method then fulfills a function in gene conservation (Marquardt 1957).

#### *Progeny-tested clonal orchards*

Orchards of this type contain a large number of clones obtained through plus-tree selection and grafting. Progeny are tested after open or controlled pollination, and the orchard is rogued on the basis of results, only the best clones being left. A large genetic gain may be expected (Namkoong et al. 1966). The method is a useful first step in a continuing selection program and provides genetic information (heritabilities, genetic correlations, genetic gains) from the analysis of the progeny tests as well as material for the next cycle of selection (Johnsson 1964).

### *Seedling seed orchards from open pollination*

Species that flower early in nature (e.g., black spruce, jack pine) lend themselves to this approach, and also those that are subject to scion-rootstock incompatibility such as Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) (Goddard and Brown 1961; Orr-Ewing 1969). Seed is collected from open-pollinated plus trees, and seedlings are established in plantations designed for seed production. Some seedling seed orchards have been developed with the intention of combining progeny testing with seed production (Wright and Bull 1963), but this is not generally possible since the two functions are basically incompatible (van Buijtenen et al. 1971). Progeny-testing should be carried out on the basis of normal spacing and rotation periods, but seed production should start as early as possible and spacing adjustments have to be made. Furthermore, a single combined progeny test-seed orchard is methodically inadequate since it does not permit the exclusion of the genotype-environment interaction. Another complication is that all seedlings derived from the same mother tree are related; hence, to avoid inbreeding, when a plot is thinned to increase spacing and crown surface for improved seed production, only one tree per plot should be left. The only way to overcome all these difficulties is to use different designs for the progeny tests and seedling seed orchards: in a series of plantations with the same progenies, all except one or two should be designed for progeny-testing; the remaining one or two plantations should be laid out to allow for seed production after thinning on the basis of the test results.

### *Seedling seed orchards from controlled pollination*

After phenotypic selection of plus trees in the forest, subsequent seed and scion collection, and grafting and establishment of clone banks, controlled pollinations are performed on the original parents or their grafts in the clone bank. The progenies from these pollinations are then established in plantations. To carry out both progeny-testing and seed production, the same design problems must be solved as in open-pollinated orchards. This method promises greater genetic gains than the method based upon open pollination (Namkoong et al. 1966) but is costlier and requires more-specialized personnel and facilities.

### *Other selection methods and orchard types*

Several additional selection methods based on plus trees may be applied, some being merely variations of those already mentioned (Libby 1969a; Namkoong et al. 1966; Shelbourne 1969a). A simple method developed in the Pacific Northwest (Silen 1966 and footnote<sup>1</sup>) consists in selecting several hundred parents, which are marked and preserved, followed by

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<sup>1</sup>Silen, Roy R. 1971. Progressive tree improvement program for Douglas-fir. West. Forest Genet. Assoc., Univ. Wash. (Seattle), Aug. 1971. 12 pp. mimeogr.

open-pollinated progeny testing over a number of decades. Because it starts from a broad genetic base, the method is flexible and offers choices in testing several characters over a period of time, thus avoiding a dead end that may result if a program is initiated with only several dozen phenotypes and based on few characters, the economic importance of which may change. A part of the program is the controlled crossing of all parents in a "biparental" mating scheme, in which each parent is mated only once to any other parent. For example, with a total of 300 parents, this requires 150 crosses. A broad genetic base is maintained in this way. The progeny from these crosses is then established at close spacing in plantations that will be converted to seedling seed orchards on the basis of the results from the open-pollinated tests.

In the program of the British Forestry Commission, plus-tree selection is combined with seed collection from plus trees that flower, and this is followed by grafting of scions into clone banks. Before seed orchards are established, the open-pollinated seed is used to make progeny tests for the purpose of excluding the clones of low value (Fletcher and Faulkner 1972).

#### THE INTEGRATION OF THEORY IN PROGRAM DEVELOPMENT

The development of a plus-tree selection program requires the integration of theory and methods from several disciplines - e.g., genetics, mensuration, soils, site classification, silviculture, wood science, and utilization. This section deals with this integration only in a general way since detailed prescriptions depend upon individual species or even regions within a species' range. Only the major phases of a program will be discussed.

##### Geographic Framework

One of the first steps in any silvicultural and breeding program with native species is the delineation or recognition of ecological regions, breeding districts, or seed zones (Hills 1959; Haddock 1962; Fowler and MacGillivray 1967; Klein 1968). A further subdivision into ecological units, or the use of existing management units in selecting and registering plus trees, is also required. These regions (and their subdivisions) are needed for the following purposes:

1. To control the movement of seed and planting stock and thus to maintain high survival, hardiness, and good growth. Crop security is one of the breeder's basic objectives, more important than any other consideration and easily applicable to large areas (Stern 1960).
2. To calculate annual seed requirements for the area to be regenerated and hence the acreage of seed orchards to be established in each region. Since a minimum number of clones is required per orchard to avoid inbreeding, the number of regions and clones per orchard together will

determine the minimum number of plus trees to be selected for each species (as indicated in the section starting on page 17, the number of plus trees to be selected for a breeding program will generally be larger than the number established in seed orchards).

3. To develop standards of plus-tree selection. These must be based upon the growth of a species in different forest types and sites, and will therefore vary from region to region.
4. To plan progeny-testing systematically within regions, by means of information on the origin of plus trees in relation to ecological or management unit or stand. Such subsidiary information can greatly improve estimates, but the neglect of seed zones or ecological regions in progeny-testing leads to unrealistic heritability estimates (Stern 1960, 1962) and therefore to unreliable predictions of genetic gain.

### Stand Selection

Within the ecological regions, selection starts with the designation of suitable stands (Fig. 5). The distribution of stands should take account of the presence of forest types and ecological units as reflected in forest-inventory and site-classification data. The designation of suitable stands is facilitated if some information is available from provenance experiments, particularly if these experiments are based on representative samples and long-term performance records.

The point has been made that stands should be chosen on several site classes to avoid selection of trees adapted to a narrow range of milieus (Brown and Goddard 1961). This suggestion should have particular merit where a species occurs in isolated stands and differences in gene frequencies exist, as in southern stands of white spruce growing in granite or limestone areas (Farrar and Nicholson 1967; Teich and Holst 1974). In some northern species, which grow over a broad range of sites, isolation is not common. In boreal black spruce, for example, adaptation to bog and upland sites could not be demonstrated (Morgenstern 1969). In these circumstances, therefore, little is gained by selecting stands on poor sites, where the expression of genetic differences from tree to tree will be inhibited. On the contrary, a case can be made here to select stands only on the better sites, where the expression of genetic diversity is favored. Selection of stands primarily on the better sites is also justified because these are the sites that will have priority in regeneration programs.

The age of the chosen stand is important. Selection in stands of present rotation age will not lead to the identification of genotypes that perform best under management conditions. It is expected that in plantations, site preparation and control of density and weed competitors will lead to more rapid growth and shorter rotation periods than in natural stands (Stiell and Berry 1967). The types that inherit the capacity for rapid growth at an early age are desirable as members of future stands.





*Figure 5. A stand of white spruce along the Gurney forest-access road, northeast of Kapuskasing, Ontario. Because of the scattered occurrence in northern Ontario of stands with a large white spruce component, knowledge of the area and accessibility will favor the development of a selection program.*

For these reasons the selection of middle-aged stands, close to expected future rotation periods, is the best solution (Heaman 1963; Sidhu 1972).

If a choice is to be made between even-aged and uneven-aged stands, the former should be preferred because they allow more accurate tree comparisons (Fig. 6). From this point of view plantations are ideal, provided the seed source is known (Rudolf 1956). Plantations of unknown origin are acceptable only if the opportunity for selection in native populations is very limited and there is good evidence that the expected gains are large enough to justify a certain risk.

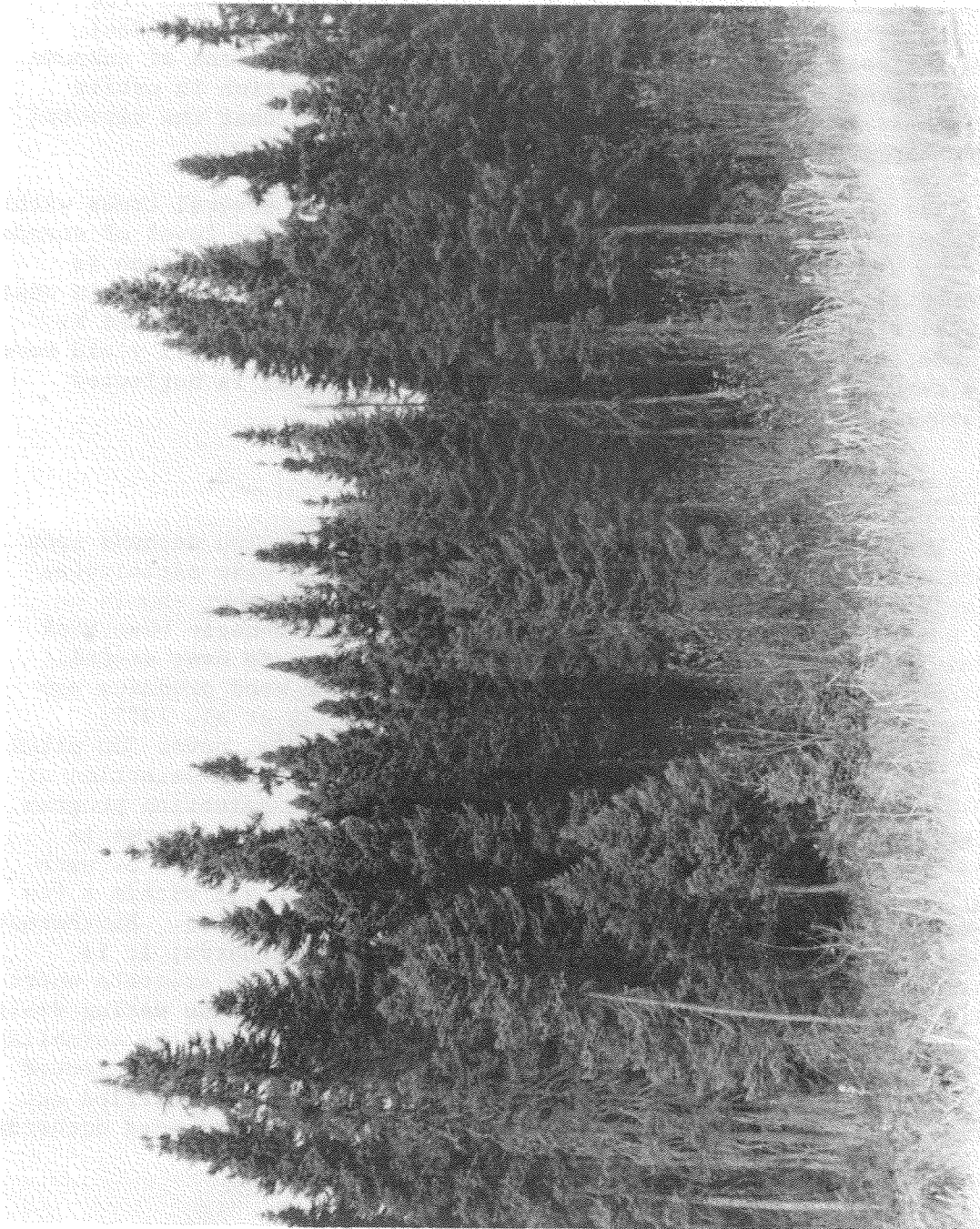
The selection of stands within regions and of several trees within stands permits the utilization of genetic variation at the level of stands. Two factors are involved. One is that if stand-to-stand variation is large, selection in the best stands will be profitable. The other is that, in the analysis of progeny tests in which the progenies are grouped by stands, the calculation of heritability can be refined and will yield more reliable results than in experiments in which this level is neglected (Stern 1960; Libby 1965).

#### Number of Plus Trees per Region

The number of plus trees to be selected per region depends upon the overall breeding plan for a given species. If the plan anticipates selection and breeding over several generations, this number should be large. A large number of plus trees provides a broad genetic base that will avoid inbreeding and allows genetic gains to be made over several generations even if silvicultural systems change, new wood products are being sought, and new diseases are introduced (Bingham et al. 1971; Franklin 1972). As some regions in Ontario, for example, cover 300 miles east to west and 150 miles south to north (Hills 1959), the selection of 200-300 plus trees is not excessive. The white spruce selection program in northern British Columbia (Kiss 1970) and the jack pine program in Manitoba and Saskatchewan (Klein 1968) anticipate the selection of such numbers in each region. The trees need not be selected all within a few years but could be accumulated gradually over a longer period. Furthermore, it is not necessary to establish all of them in seed orchards; it is necessary, rather, to keep them in clone banks or breeding arboreta where controlled pollination can be undertaken according to certain mating designs. To produce improved seed at an early stage, seed orchards can be established soon after the initiation of the program from a fraction of the selected population. In this way breeding and seed production can be carried out separately, and new gene material can be introduced into the seed orchards at any convenient time (Zobel et al. 1972).

#### Number of Clones per Seed Orchard

To avoid inbreeding, each seed orchard should consist of at least 20-30 clones or genotypes (Stern 1959). Twenty clones may be inadequate if species differ so greatly in onset of flowering from clone to clone that





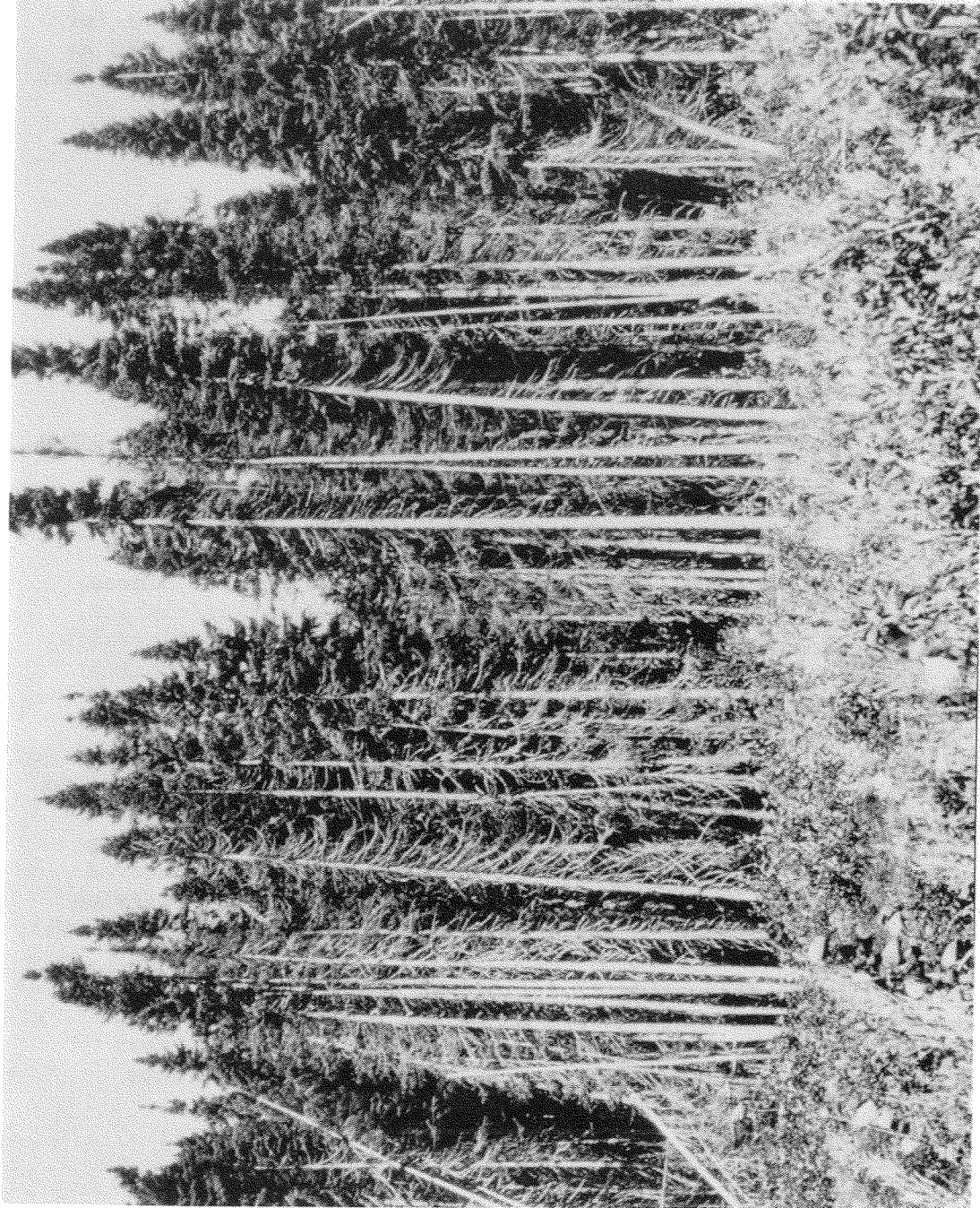


Figure 6. Stand selection in black spruce. The stand on page 18 is uneven-aged and grows on a moist site near Cochrane, Ontario. Slow growth may have inhibited the expression of genetic differences, and plus-tree selection would be difficult. The stand on page 19, from near Kapuskasing, Ontario, is situated on a fresh site and grows rapidly. It is more suitable for plus-tree selection.

only a fraction of the established clones actually contributes to seed production during the early years of orchard development, or if the flowering period in a certain species and region extends over several weeks and sufficient overlap does not exist among all clones. In such cases a larger number of clones is needed to allow a selection for flowering time within the orchard. If 40-90 clones are established, selection for flowering time and roguing on the basis of progeny-test results could be practised by either leaving the orchard for continued seed production with larger genetic gains or establishing a new orchard.

### Choice of Traits

The choice of traits is a major topic in the development of a selection program, and only some principles will be discussed here as an introduction to the problem. This introduction will reflect the close cooperation needed between various disciplines.

Selection should be restricted to very few traits (Campbell 1964). Additional traits may increase the effort and cost disproportionately, particularly if the genetic correlation is zero or negative. On the other hand, selection for a single trait is usually not possible in species utilized for a variety of forest products. This then leads to some form of multiple-trait breeding (Stonecypher 1970).

Traits with long-term economic value should be chosen. These are probably such traits as growth rate, form and stem characteristics, specific gravity, and insect and disease resistance. In general, traits subject to the whims of fashion (e.g., certain grain patterns in birch and maple) should not be chosen, unless good progress can be made in a short time, or a minor or localized effort is involved. It should not be assumed that breeding is a substitute for silviculture; usually they go hand in hand. Sometimes silviculture alone will be sufficient to improve a certain wood product. It is also unwise to initiate an expensive breeding program for a particular wood property, possibly anticipating several generations of selection, when the same result can be achieved within a few years by improved industrial technology, e.g. by modifying fiber length through refining processes in the mill (Reid and Ladell 1965).

The following discussion of individual traits based on the literature is not restricted to trees native to Canada (where the available information is limited). The experience applicable to some selected Canadian tree species will be summarized in the second part of this publication.

#### *Growth rate*

Growth rate, as expressed by volume growth of the individual tree, is traditionally determined by age, height, diameter at breast height, and form class. Height growth is strongly affected by environment. It is, for example, the basis for site-class designation. Selection for height

is difficult (Stephenson and Snyder 1969), but height is less affected by competition than diameter (Weck 1954).

It has been emphasized that in selecting for growth rate selection should be directed toward finding not the largest tree but the tree that has utilized growing space, light, and nutrients most efficiently. This requires finding the tree with the best growth in relation to its leaf surface area (Rudolf 1956; Brown and Goddard 1961; Campbell and Rediske 1966). A technique to apply this concept will be discussed in the subsection describing the base-line system.

When a similar concept was applied to Norway spruce (*Picea abies* [L.] Karst.), it was found that the greatest volume on a unit area of land is produced by a stand composed of many fast-growing trees with moderate diameters and slender crowns (Etverk 1972).

Even though selection in the forest has been based upon a variety of methods, results from the first progeny test of southern pines indicate that selection for growth rate has been successful and that improvements of 10 to 50% have been achieved over random material (Zobel et al. 1969).

#### *Wood quality in relation to pulp and paper properties*

Wood quality traits, such as specific gravity, fiber properties, and content of lignin, holocellulose, and alpha cellulose, vary widely within the same population, are correlated phenotypically in many ways, and often are strongly inherited (Reck 1965, 1969; Kennedy and Warren 1969; Namkoong et al. 1969; van Buijtenen 1969a; Ladell 1970). Theoretically, good opportunities exist for improvement of wood quality by breeding.

Nevertheless this potential is not easily utilized in the short run. The type of pulp manufactured varies from mill to mill, and the economical effect of individual wood-quality traits is rarely known in detail (Namkoong et al. 1969). It may be easiest to select initially for growth rate and anticipate selection for most other wood-quality traits in the second generation, i.e. the progeny tests arising from the first-generation selections. Specific gravity could be included as a selection criterion in the first generation by taking increment cores and subjecting them to rapid analysis by automated X-ray densitometry (Kennedy 1970) so that specific gravity could be taken into account before the final selection was made. This approach is feasible in such diverse species as loblolly pine (*Pinus taeda* L.) (Zobel et al. 1969) and white spruce (Chang and Kennedy 1967), because the correlation between volume and specific gravity was either not negative or so small that it could be neglected. Even with a substantial negative genetic correlation between volume and specific gravity ( $r = -0.54$ ) as in European black pine (*Pinus nigra* Arn.) the relative loss in specific gravity in selection for volume alone was not appreciable (Arbez and Millier 1972).

### *Stem and branch characteristics*

In pulpwood, stem eccentricity and nodal swellings add to the cost of bark removal. Extremely crooked bolts also cause trouble in chipping. The size and angle of branches affect the volume of knotwood and the volume of compression wood. Chemical pulping is hindered by the number and size of knots, which are difficult to digest. In groundwood pulping, nodal swellings and knots prevent even packing of bolts and cause losses in grinder efficiency (Faulkner 1969; Shelbourne 1969b).

Log quality, mill output, and end products like veneer, lumber, poles, and posts are adversely affected by sweep, crook, bole spiralling, forking, narrow branch angle, heavy branches, and knots (Clausen and Godman 1967; Dobie 1964; Faulkner 1969; Shelbourne 1969b).

Wide variation in these tree characters is reported from many species, and heritabilities determined have been moderate to high. Even with ocular selection of plus trees in the forest, selection promises to be efficient (Magini 1969; Shelbourne 1969b; Zufa 1969).

### *Insect and disease resistance*

In a plus-tree selection program aimed primarily at the improvement of yield and quality, only trees free of damage from insects and diseases should be selected. In general, native species coexisting with native insects and diseases possess an adequate level of resistance resulting from a balanced relationship in a host-parasite system (Bingham et al. 1971; Heimburger and Sullivan 1972). In such a system, perfect resistance does not exist, but silviculture plays an important role in control of losses by attention to provenance, avoidance of off-site planting, and removal of large areas of overmature forest and dead and dying trees left after natural catastrophes.

On the other hand, breeding for insect and disease resistance is a specialized activity that should be distinguished from a general plus-tree selection program. This may require the application of special selection and test procedures, provenance and species hybridization, mass vegetative reproduction, etc. (Heimburger 1962; Soegaard 1964; Gerhold 1970; King 1971).

### Selection Procedures in the Forest

The procedures to be used for selection of plus trees in the forest should be adapted to the particular problems of each species. They will depend upon the type and number of traits considered and their heritability, the selection intensity, the stand structure (even-aged or uneven-aged), the propagation method used in orchard establishment, and other variables. The following description of procedures is based mainly on van Buijtenen (1969b). A critical review has been presented by Ledig (1973).

### *Ocular selection*

The simplest procedure is ocular selection. Vigorous, healthy trees of good form and size are rapidly identified without measurement or rating of individual traits. The procedure may be adopted because the heritability of the traits considered is so low that much progress in selection can only be made through efficient progeny tests; or it is so high that carriers of suitable genes can be easily identified, so that detailed comparisons are made unnecessary. It may be applicable only when selection is restricted to very few traits.

### *Comparison trees*

The candidate tree is compared with its nearest neighbors, or the average or best tree in a stand, in such traits as height and diameter at a given age, stem form, branch angle, etc. and must be superior in one or more traits. The procedure is efficient in plantations and even-aged natural stands, but may be less efficient than other methods if neighbors are related (Snyder 1969, Ledig 1974). It would be unsuitable in species that reproduce vegetatively, such as aspen or black spruce, unless clones could be easily delineated. The comparison-tree method is commonly applied in the pine forests of the southern United States (van Buijtenen 1969b), in spruce plantations in Great Britain (Fletcher and Faulkner 1972), and in the selection of Douglas-fir, western hemlock (*Tsuga heterophylla* [Raf.] Sarg.), and lodgepole pine (*Pinus contorta* Dougl.) in British Columbia and the Yukon Territory (Walters et al. 1960; Heaman 1963, 1967; Sziklai 1970). A variation of the method was used in the selection of sugar maple (*Acer saccharum* Marsh.) plus trees in the northeastern United States by taking rapid hand refractometer readings of the sugar content of sap of individual trees and their neighbors located along transect lines. After identification of candidates by different fieldmen, the final selection was made by a geneticist, who considered additional traits such as diameter, height, crown form, and insect and disease damage. This final screening eliminated five out of every six trees initially identified by fieldmen (Gabriel 1972).

### *Base-line system*

Growth, or any other dependent variable of a species on a given site, is measured together with an independent variable on at least 10 check trees. The regression of the dependent variable on the independent variable is obtained. Candidate trees must exceed the mean of the base population by a certain amount, e.g. two standard deviations.

Selection for growth efficiency is done by this method, in which not the largest tree is being sought but the tree that, on a comparable site, grew best in relation to its leaf surface area (Brown and Goddard 1961). Accordingly, one approach is to determine in each stand the regression of breast-height diameter squared x height on crown diameter x crown length. Trees above the regression line reflect special vigor and can be selected (Rudolf 1956). A similar procedure is to measure basal



area increment for a certain period, e.g. 10 years, and relate this to the product of crown length x radius. Again, trees above the general regression line are candidates for selection. Dale (1962) has given a simplified procedure to calculate crown-surface area. These measurements of the relationship of crown size to growth are relatively time-consuming and are being made only if the candidate tree meets minimum requirements in crown and branch characteristics and is free of damage from insects and disease (Brown and Goddard 1961).

### *Absolute standards*

Absolute standards are set by a local volume table, a regional yield table, or tables showing the distribution of a single trait or several traits combined (Trimble and Seegrist 1970). After the establishment of the site class upon which the stand grows, measurements are made on apparent candidates to determine whether they exceed the standard by the required amount, e.g. so many feet or standard deviations in height at a given age. This procedure has been applied in the selection of black spruce in northern Ontario (Carmichael 1960).

In the selection of Norway spruce plus trees, Etverk (1972) calculated their productivity from the following formula:

$$Z = \left( \frac{D}{D_v} \right)^2 \cdot \frac{0.39 H + 0.34}{\alpha}$$

where  $Z$  is the mean annual stand increment in  $\text{m}^3$  per hectare (ha) per year;  $D$ , the breast-height diameter in cm;  $D_v$ , the crown diameter in m;  $H$ , the height in m; and  $\alpha$ , the tree age in years.

Candidate trees should have a minimum  $Z$  value of 12 to be admitted as plus trees. They would then represent the average tree to produce 12  $\text{m}^3$  per ha per year in stands of 1.0 density on the best site class at approximately 50 years of age. Studies indicated that trees making up such stands would be characterized by fast height growth, moderate diameter increment, and narrow crowns.

The method of absolute standards has also been defined as one in which a point score based on several traits must be reached before a candidate tree can be accepted. It has been found useful in hardwood stands, which are usually uneven-aged, and where comparison trees nearby are not available (van Buijtenen 1969b).

### Recording Forms

Numerous forms for the recording of field data and measurements have been developed and in some cases integrated with a record system useful in subsequent progeny-testing (Bouvarel 1955; Bolland and Hoffmann 1959; Walters et al. 1960; Ontario Department of Lands and Forests 1963; Plym Forshell 1964; Heaman 1967; Sziklai 1970; Fletcher and Faulkner 1972; Gabriel 1972). An "Initial Tree Selection Form" developed by the Texas

Forest Service (Brown and Goddard 1961) incorporates the useful provision of checking for 10 minimum requirements covering total height, diameter, stem form, branch angle, and absence of damage from insects and diseases, which is preferable to a subjective rating. Detailed measurements need then be made only on those trees that meet minimum standards. Fig. 7 depicts the general form used at Petawawa Forest Experiment Station. This can easily be modified to meet specific problems in individual species.

### Conclusions: Elements of a Program Plan

The review of genetic concepts has indicated that the success of plus-tree selection depends upon the variability of the trait in question, the correlation between genotype and phenotype (i.e. trait heritability), and the selection intensity applied, as shown in the response equation,  $R = i\sigma_p h^2$ . Furthermore, it has been shown that plus-tree selection can be fitted into several breeding methods that may differ in efficiency. Needless to say, the goal is to achieve maximum response per dollar or unit of time. In the choice between several alternatives, mathematical programming may be applied and this need not be very complicated (van Buijtenen 1969b; van Buijtenen and Saitta 1972). A realistic appraisal of the practical problems encountered in a plus-tree selection program and information on the economics of the various operations is also very important, in addition to the genetic and other parameters used in the response equation (Johnsson 1964).

The steps necessary in a selection program for a particular species may be summarized as follows:

1. Choose the characters to be improved.
2. Examine the variation pattern of the species concerned to determine at which level selection is to be concentrated. For example, if experiments on geographic variation indicate that stand-to-stand variation is large and tree-to-tree variation within stands small, it will pay to concentrate selection at the stand level and devote less effort to selection within stands.
3. Decide whether mass selection in the forest or progeny testing is to be emphasized. The decision is based on heritability. For example, high heritability of a given trait favors high-intensity selection in the forest, while low heritability would make high-intensity selection in the forest very costly and a better return from progeny tests would be expected.
4. Fit plus-tree selection into the overall breeding program for the species, considering the number of plus trees needed; the timing of selection if scions, seed or both are to be removed; the amount of seed required per tree if open-pollinated progeny testing is planned; the physiology of the species (e.g., scion-graft compatibility) and anticipated methods of orchard management; and the number of seed orchards and total seed requirements in an ecological region, which are based upon the silviculture of the species.

<b>Purpose:</b>											
<b>Species:</b>								<b>Map No.:</b>		<b>Ortet Photo:</b>	
<b>Location in detail:</b>											
<b>Description of stand:</b>										<b>Ramet Photo:</b>	
<b>Soil:</b>											
<b>Flora:</b>											
<b>Climatic Region</b>				<b>Lat.</b>		<b>Long</b>		<b>Elev.</b>			
<b>Year</b>	<b>Date</b>	<b>S/P1.</b>	<b>Age</b>	<b>Height</b>	<b>D.B.H.</b>	<b>Bole H.</b>	<b>Knot <math>\angle</math></b>	<b>Crown D</b>			<b>Name</b>
<b>Axis:</b>								<b>CONTROL TREES</b>			
<b>Bole:</b>								<b>No.</b>	<b>Ht.</b>	<b>D.B.H.</b>	<b>Age</b>
<b>Bark:</b>								1			
<b>Branches:</b>								2			
<b>Crown:</b>								3			
<b>Spacing:</b>								4			
<b>Health:</b>								5			
								6			
								7			
								8			
								9			
								10			
<b>Periodic Radial Increment in mm:</b>											
<b>10</b>	<b>20</b>	<b>30</b>	<b>40</b>	<b>50</b>	<b>60</b>	<b>70</b>	<b>80</b>	<b>90</b>	<b>100</b>		
<b>110</b>	<b>120</b>	<b>130</b>	<b>140</b>	<b>150</b>							
<b>1</b>	<b>2</b>	<b>3</b>	<b>4</b>	<b>5</b>	<b>Location:</b>						<b>Clone No.:</b>

Figure 7. Plus-tree record form used at Petawawa Forest Experiment Station. The back side of the form contains provision for cross references to the scions and seed subsequently grafted or sown.

Because of the size of the areas to be regenerated in many regions of Canada, it is well to realize that, in this generation, only a beginning can be made in a continuing program of selection and breeding. Flexibility permitting change of goals and procedures should therefore be an important element in all breeding programs. Once the breeding strategy has been developed, it is necessary to familiarize top management with the broad issues so that adequate support is maintained (Namkoong et al. 1971).

In the past, many plus-tree selection programs have been started without due consideration of all these questions. The genetic information available was always incomplete and based on small samples or even analyses incorrect by present standards (Namkoong et al. 1966). In spite of these problems, the results achieved have often been encouraging (Zobel et al. 1972), and this should give impetus to those who consider new programs. Nevertheless, each program encounters specific problems and a careful evaluation of all available information is necessary to reach the objectives and use available resources effectively.

# OUTLOOK FOR SELECTED SPRUCES AND PINES IN CANADA

## WHITE SPRUCE

by

A.H. Teich

### Introduction

The purpose of this section is to propose plus-tree selection for producing rapidly growing, genetically improved white spruce (*Picea glauca* [Moench] Voss) for the urgent needs of the future, and to suggest procedures that will favor the effectiveness of selection and utilization. There is little improved seed available to satisfy planting requirements in Canada. The need for such seed is most urgent in central Canada (much of the forestation with white spruce has been in Ontario and Quebec) (Cayford and Bickerstaff 1968) and in British Columbia (Dobbs 1972).

White spruce plus-tree selection is now appropriate. Extensive seed source studies, initiated from the mid- to the late 1950's, have led to the identification of many rapid-growing races for much of eastern and central Canada. Use of seed from random trees of these seed sources rather than local seed would increase height growth by an average of 15 to 20% (Teich 1970b). Additional increases are possible. By selecting the tallest 10% of the trees in each seed source, height growth can be increased an additional 5% without progeny-testing and 10% with progeny-testing (Holst and Teich 1969). Since the rapid-growing races must be propagated in seed orchards to increase the seed supply, it is desirable to propagate only the best trees. The cost of selection is small in relation to the expected gain.

An essential question that must be asked is: does plus-tree selection in white spruce pay ... do the benefits justify the costs? A cost-benefit study of white spruce genetic improvement produced an estimated benefit of \$832,000 a year for a 15% increase in growth rate in the national context (Carlisle and Teich 1971). A 5% increase in growth rate by plus-tree selection alone (Holst and Teich 1969) would therefore yield an annual return of \$277,000, which should easily support the plus-tree selection component of an integrated improvement program consisting in seed-source selection, plus-tree selection, progeny-testing, and seed-orchard establishment and management.

### Population Structure

As in other species, in white spruce there are forces that tend to cause genetic differentiation of individual trees and stands from the species average, and forces that tend to bring progeny of deviants back

toward the species average. The major forces leading to differentiation are mutation, selection, and "genetic drift" (the tendency of very small groups such as small isolated stands to deviate from the population norm). Cross-pollination within and among stands and seed dispersal tend to reestablish gene frequencies in subpopulations similar to those of neighboring populations. Consequently, where a large area is covered by white spruce and where there are no barriers to pollen or seed dispersal, individual trees selected within that area tend to differ little, genetically. On the other hand, where trees grow widely scattered or in small isolated stands, individual trees or stands tend to deviate even from their nearest neighbors.

White spruce stand distribution differs across Canada. In the east, trees commonly grow as individuals in abandoned farm fields, and in small, mixed stands. In central Canada most white spruce stands are small and often effectively isolated from other white spruce stands. Only in the west and northwest are large pure white spruce stands commonly found. This isolation in areas other than the west and northwest has led to extensive genetic differentiation among stands and among trees within stands. Differentiation among and within stands has been explored very little, but all the results are consistent with extensive genetic variation (Jeffers 1968; Nienstaedt 1968; Holst and Teich 1969; Teich 1970b; Nienstaedt and Teich 1971; Pollard and Teich 1972).

The genetic variation among and within stands has ramifications of considerable consequence in white spruce breeding.

1. When a valuable seed source is identified, it must be precisely defined because closely adjacent stands may differ.
2. Because most stands are small, their seed productivity is usually inadequate for widespread use. Seeds must be produced in orchards.
3. Some seed from rather isolated trees results from self-pollination and will produce slow-growing seedlings. These must be culled in nurseries.

#### Choice of Traits

Most white spruce harvested is processed into pulp, and the principal concern is to harvest the most cellulose per acre. There is a growing demand for increased wood quality for sawlog production. The main emphasis in selection should be on visual estimates of a tree's merchantable volume. In this estimate the dominating factor is stem volume, but secondary factors such as stem straightness, fine, horizontal branching, narrowness of crowns, and a small degree of stem taper, all of which are associated with net timber yield and quality, should also be considered as favorable. Some desirable phenotypic characters ought to be ignored because they are not heritable. This probably applies to freedom from spruce budworm (*Choristoneura fumiferana* [Clem.]) and damage by mechanical equipment, herbicides, and salt. Any attempt to select for characters of low heritability or of low value is usually at the expense of improvement in the more desirable characters.

A tree with acceptable stem, crown, and branch form is shown in Fig. 8.

### Strategy of Selection

It is advantageous to select plus trees in a good or medium seed year. Stands and trees can be located in the spring and early summer, but selection is best from mid-August to early September, when ripe seed can be collected at the same time. The advantages are:

1. one may select against low seed production;
2. seed can be collected for progeny tests;
3. surplus seed can be used in production nurseries, their extra value being credited against the cost of the breeding.

Selection in a poor seed year is possible, but these advantages must be foregone.

Intensity of selection, i.e. how many trees are examined for each tree selected, is a major factor in determining the amount of gain achieved. From published (Holst and Teich 1969) estimates of genetic variation in white spruce growth rate and heritability, the following genetic gains in growth rates are expected at the given selection intensities:

	<u>Intensity of selection</u>				
	selecting 1 out of				
	2	10	20	100	1,000
Expected gain in height growth rate - %	2.4	5.4	6.0	9.0	9.9

The expected additional gains with higher intensities diminish rapidly. It is obvious that selection intensities above one in 100 are not highly rewarding.

The absolute number of trees to select (as distinct from selection intensity) is a major consideration for which there is no reliable research result for guidance. It is natural to want to include as many fine trees as possible. Inbreeding, a harmful process, is minimized, and genetic variation among selections is high, conferring upon the selected group adaptability to a variable environment.

However, selecting few trees results in a higher average value for the selections as a group; selecting only a single tree means that only the best one is selected. As the number of selections increases the average value of the selections is reduced.



*Figure 8. A white spruce plus tree selected near Iroquois Falls, in northern Ontario. Note the straight stem, narrow crown and wide branch angle.*



The number of trees to select is therefore a compromise. Twenty trees are usually accepted as the minimum. Alleles as rare as one in 100 would have at least a 56% probability of being retained. As a proportion of the plus trees will be rejected before orchard establishment, at least 4 times as many trees (80) should be selected initially.

### Test Procedures

Plus trees ought to be grafted for vegetative maintenance during the time that progeny are being tested to provide a scion source for propagating the selections for seed orchards.

For greenhouse grafting the rootstocks should be potted in the late spring after at least 8 weeks of chilling at about 2°C (Nienstaedt 1966). A period of 2 or 3 weeks in the greenhouse prepares the stock plants for grafting by stimulating root growth. Scions should be grafted high on the stock and the lower stock branches retained for 3 or 4 years. Scion growth of the grafted plants is promoted by an 18- to 20-hour photoperiod.

A nursery test is a rapid and effective means of testing plus trees. In white spruce, early superiority tends to persist (King et al. 1965; King and Rudolf 1969). A 4-year test of 100 seedlings per progeny, in 25-seedling randomized plots, will likely permit rejecting half of the plus trees with little danger of losing any extremely good ones. A field experiment with the selected progenies with a similar number of seedlings and replications will probably allow culling half of the remaining plus trees.

### Seed Production

Grafted seed orchards are preferred to open-pollinated seedling seed orchards because the grafted tree is a genetic reproduction of the plus tree, while the seedling is likely a hybrid of the selected tree with an ordinary tree. Also, grafted trees produce seed sooner than trees grown from seed.

The logistic considerations in seed orchard establishment are tree spacing, seed yield per acre, and productive life of a seed orchard.

Seed production in white spruce grafted seed orchards has been described by Nienstaedt and Jeffers (1970). A 7-acre seed orchard planted at 15 by 15 foot spacing would yield enough seed for 4 million plants within 10 years of grafting. The orchard would subsequently be thinned to 30 by 30 foot spacing and would then yield enough seed for 1 million plants. An acre of seed orchard at the latter spacing would therefore produce enough plants for about 210 acres at an 8 by 8 foot (681 per acre) spacing. Seed orchards can most likely remain productive for many years, but they will probably become obsolete about 30 years after establishment, when second generation selections can be used for additional improvement.

A "ball park" estimate of the logistics of selecting and utilizing plus trees is provided by the following simplified, hypothetical example based on realistic data.

A province with a projected annual planting program of 70,000 acres a year is divided into seven site regions. An average region, in which 10,000 acres a year are planted, must have a seed orchard with an area of about 50 acres to produce adequate quantities of seed. Each acre of orchard will cost (van Buijtenen and Saitta 1972) about \$365 to establish and \$107 a year to manage during a 30-year lifetime of which 20 years will be productive. Added to this will be the cost of initially selecting the 20 trees, estimated at \$170 a tree. Amortized over the 20 productive years, the annual cost of a 50-acre orchard will be about \$9,107. The returns from using the improved seed on a site of average quality with an assumed increase in merchantable volume of 9% will be about \$50,000 (Carlisle and Teich 1971) - in effect a \$5 return for each dollar invested.

### Conclusions

Plus-tree selection is a worthwhile means of improving white spruce growth rate. Plus trees are the best source of scions for establishing grafted seed orchards to ensure adequate seed production and rapid growth of the resulting seedlings. A selection intensity of about one plus tree for every 100 is suggested, and at least 20 of them would have to be established in each orchard to control inbreeding and retain adequate genetic variability. One acre of seed orchard will likely supply about 210 acres of annual planting. The entire cost of producing improved seed will probably be very little compared with the value of the increased growth of the improved seedlings.

# BLACK SPRUCE

by

E.K. Morgenstern

## Introduction

Black spruce (*Picea mariana* [Mill.] B.S.P.) is the most valuable pulp and paper species in the Boreal Forest Region (Rowe 1972), where it is utilized and regenerated artificially on a large scale (Heinselman 1957; Vincent 1965; Tucker and Ketcheson 1973). From 1969 to 1973 about 30 million trees, or at least 30,000 acres, were planted annually, mainly in Ontario and Quebec (Campagna and Fortin 1970; Lane 1970). An additional area of unknown size was regenerated by direct seeding. Predictions are that the regeneration program will be expanded considerably (Cayford and Bickerstaff 1968).

Since 1952 a modest genetic research and breeding program has been conducted by the forest industry, provincial forest services, and the federal Canadian Forestry Service (Carmichael 1960; Johnston 1963; Humphreys 1966; Corriveau 1971; Fowler et al. 1971; Klein 1971; Morgenstern 1973b) and some factors basic to the development of a selection program have been sorted out. Black spruce begins to flower when about 6 years old (Morgenstern and Fowler 1969); hence flowering age will not limit selection but rather the time required for progeny tests. An early progeny test has shown that a genetic gain of 8% could be made even in a small population (Morgenstern 1973a). The seed orchards developed in northern Ontario by Spruce Falls Power and Paper Company and Kimberly-Clark of Canada Ltd. have not given any evidence of scion-rootstock incompatibility but have shown that high-quality seed can be produced both in grafted clonal and seedling seed orchards (personal communication from R.H. Armstrong and J.A. McPherson). Therefore, the size of the regeneration program, the genetic information, and the initial breeding experience all indicate that black spruce selection is promising and that no time should be lost in putting it into practice on a larger scale. In the United States, where black spruce is important only in the Lake States, conclusions were similar (Dawson and Pitcher 1970). Since breeding is a cost added to the price of seed, large benefits can be obtained from a relatively small investment per unit area (Bouvarel 1966; Carlisle and Teich 1971).

## Population Structure

In the boreal forest black spruce occurs on a broad range of sites, from wet to dry moisture regimes, and in pure as well as mixed stands. It is one of the most common species, and little isolation exists between stands in bogs and those on upland sites. Changes in gene frequencies that

exist are likely caused primarily by natural selection for day length and temperature, while local factors such as soil moisture and local climate play only a minor role. The resulting population structure is marked by gradual changes in phenology and growth parallel to gradients in latitude and temperature and by relatively minor differences between stands locally or even within a region (Morgenstern 1969).

More recent experiments at Petawawa have again supported these conclusions. Among single-tree progenies from different stands in the same region, most of the variation was concentrated on single-tree progenies within stands. At the age of 2 to 7 years, the best stand exceeded the mean of all stands by only 3 to 5% in total height, but the best progeny within a stand exceeded the mean of all progenies in that stand by 11 to 27% (Morgenstern 1973a). These figures indicate that it is more promising to select carefully within stands than among stands and also that sufficient variation is available to make selection worthwhile.

### Choice of Traits

Black spruce is almost exclusively a pulpwood species. Selection should aim primarily at an improvement of dry wood-fiber weight produced on a unit area per year; i.e. a larger wood volume with higher specific gravity should be sought. The most immediate need is to select for height and diameter, which can be measured rapidly; but the weight to be given to these characters cannot be easily determined in the absence of yield tables from planted stands. The heritability of height growth on an individual-tree basis as determined in a small study was 17% (Morgenstern 1973a). This is relatively low but agrees well with the heritability obtained for other species.

Wood-quality traits have been studied in detail in a small sample (Ladell 1970), but nothing about their heritability is known. The information from other species, however, suggests that the heritability of specific gravity in general is intermediate, i.e. ranging from about 16 to about 77% (Namkoong et al. 1969). If sufficient variability is available, therefore, specific gravity could be included in plus-tree selection provided it can be assessed rapidly. Alternatively, selection for specific gravity could be delayed until plantations are available and more is known about its variation and inheritance pattern and the economic factors involved.

Present knowledge indicates that there is little incentive to consider other traits. Stem and branch characteristics need not be stressed in a pulpwood species with fairly fine branches (Fig. 9). This species is relatively resistant to insects and diseases (Basham and Morawski 1964), and these likewise require no special attention. Selection for height and diameter growth is most important.

### Strategy of Selection

In many species, plus-tree selection was initiated by intensive mass selection, a slow and costly effort at the forest stage, i.e. in



*Figure 9. Stem form in a black spruce stand at Petawawa Forest Experiment Station. Straight stems appear to be common in this species, making selection for stem form unnecessary.*

natural or planted stands. Although alternative strategies and their economics have rarely been discussed in detail (Snyder 1969; Ledig 1973), intensive forest-stage selection can probably be justified when multiple-trait selection is carried out for species utilized for a variety of products and at least some traits are strongly inherited. In black spruce the situation is different because the production of pulp is practically the only goal, and the most important traits considered (such as growth in diameter and height) appear to be weakly inherited. Given this situation, a plus-tree selection program has at least two alternatives: to aim either at a high selection intensity in the forest (to make up for the relatively low heritability) or at a low-intensity forest selection and shift of the emphasis to a progeny-test program. A cost comparison of these two approaches is given in Table 3. It is assumed that in both cases, in a given region, the immediate goal is to establish one seed orchard with genotypes of proven, superior quality (second-generation orchard). The comparison is taken to the same stage, i.e. the establishment of test plantations. The difference in approach applies only to the first selection cycle. Once seed orchards have been established with progeny-tested material, subsequent procedures can be identical.

In a program aiming at low-intensity selection in the forest, 200 trees would be selected rapidly in stands 50 to 70 years old by ocular appraisal and seed from these phenotypes collected at the same time. Since most procedures used are relatively simple, all selections could be made in one fall and winter season and grafting done in the greenhouse the following spring. Only 10 scions from each tree would be cut and grafted for a clone bank (there is no certainty that the tree is still available at the completion of the test period). Progeny would then be raised in a nursery and outplanted at eight test locations in the sixth year. One would expect to use only one of the progeny tests for seedling seed orchards, and this test should be suitably designed. The total cost of the program up to the establishment of the test plantations is \$24,000. After final measurement, 36 years after the beginning of the program, the best 20 families would be identified (10% of the initial populations). The selection intensity could be increased by selecting only the best tree in each family for establishment in a grafted seed orchard, which is also the best method to prevent inbreeding.

In the second approach, with high-intensity selection, a clonal seed orchard is established at the beginning of the program. The baseline system or the method of absolute standards should be used for plus-tree selection in the forest. The aim is to select 50 phenotypes. Not only height and diameter but also specific gravity could be included. More-intensive selection in the forest would make this operation costlier. Procedures would have to be developed more carefully, and it would take 3 years to complete the selection. The number of clones provides an opportunity for selection after progeny-test results have been obtained, and this selection makes it possible to reduce the number of clones to about one-half. Alternatively, a new orchard could be established. The total cost of forest selection, grafting, and establishment in an orchard is \$240 per clone, a figure that agrees with Bouvarel's (1966). As shown in Table 4,

TABLE 3. COMPARISON OF COSTS BETWEEN A LOW-INTENSITY SELECTION AND A HIGH-INTENSITY PROGRAM<sup>1</sup>

Category	Year	Low-intensity forest selection and open-pollinated test of wild trees	Cost \$	Year	High-intensity forest selection and control-pollinated test of orchard clones	Cost \$
Scale	-	200 phenotypes selected per region	-	-	50 phenotypes selected per region	-
Field stage	1	Selection by ocular comparison Seed collection, cutting of 10 scions	20	1-3	Selection by measurement Measurements, cutting 60 scions	60
Preparatory stage	2-5	Grafting of scions for clone bank Seed extraction, nursery production of 300 2-2 transplants per half-sib family	10 30	2-4	Grafting of scions for seed orchard Preparing seed orchard site, planting of ramets	100 80
		Subtotal per family	60	5-7	Subtotal per clone	240
		All 200 families	<u>12,000</u>		All 50 clones	<u>12,000</u>
					Maintenance of 11-acre orchard for 10 years	<u>11,000</u>
Test stage	6	Establishment of field experiments Design: 9 trees per plot, 3 replicates per site, 6' x 6' spacing, 8 test sites; area required per family: 216/1,210 = .20 acres Site preparation and planting cost \$300 per acre	60 60	11-15	Controlled pollination in orchard (biparental design), seed collection, extraction	20
		Subtotal per family	60	16-19	Nursery production of 300 2-2 transplants per full-sib family	30
		All 200 families	<u>12,000</u>	20	Establishment of field experiment from all families in the same year Design as in low-intensity program	60
					Subtotal per family	110
					All 100 families	<u>11,000</u>
	36	(Tests completed)		50	(Tests completed)	
Total cost			<u>24,000</u>			<u>34,000</u>
Annual cost to test establishment			<u>4,000</u>			<u>1,700</u>

<sup>1</sup>Man-days can be derived from the relationship 1 man-day = \$30.--. The comparison includes only expenditures to the establishment of test plantations; interest on investment and cost of equipment are not considered.

TABLE 4. CALCULATION OF THE SEED ORCHARD AREA NEEDED TO PRODUCE AN AVERAGE OF 1 MILLION PLANTABLE TREES A YEAR

Category	Number
Viable seeds per cone	13
Cones per ramet	125
Seedlings obtained per ramet	1,625
Plantable trees produced per ramet	541
Ramets needed	1,848
Ramets per acre at 16' x 16'	170
Total orchard acreage required	11

an 11-acre orchard is required to produce an average of 1 million plantable trees annually. At 16 x 16 foot spacing, each of the 50 clones could be replicated 37 times throughout the orchard by establishing its ramets (grafts). Orchard maintenance would cost approximately \$100 per acre per year (van Buijtenen and Saitta 1972), but only the first 10 years are included in the calculation, namely, the period before the establishment of test plantations. The most efficient crossing scheme is that of a modified biparental design: half of the clones are designated as males and half as females, and pollen from each male is used to pollinate four females for a total of 100 full-sib families. This stage will not be reached until about 10 years after grafting, i.e. in the years 11 to 15 after the beginning of the program. Testing begins at this stage. The experimental design used is the same as that described for the low-intensity program. The total cost is \$34,000.

Although the total and annual costs differ, a purely financial comparison is probably not adequate. In the low-intensity program, the largest effort goes into progeny-testing (including nursery production of seedlings). In the high-intensity program most of the time will be spent in initial selection and controlled pollination, and smaller numbers of trees will be progeny-tested. A big difference is found in the skills and facilities required, the requirements for the high-intensity program being much greater. It is possible that any organization considering the initiation of a new program will make its decision primarily on the basis of this difference.

#### Test Procedures

In both of the preceding selection programs, a test period of half a rotation (30 years) is assumed. The earlier results from the low-intensity program constitute an advantage in that second-generation selection can be initiated earlier. If genetic gains for one cycle of selection are



the same for both programs, the low-intensity program is preferable because genetic gain per year (Namkoong et al. 1966) is greater.

### Seed Production

Black spruce flowers at an early age and this means that seedling seed orchards are a possibility. However, in the low-intensity program, when the seed-production and testing functions are combined, and one of the eight test areas is designed for seed production, thinning of this area cannot be undertaken before the completion of the test period, i.e. about 36 years after the beginning of the program, or a few years earlier if one does not wish to await the final result. In any case, seed production from the tested progenies is attained relatively late in the program. Alternatively, in the high-intensity program, the established clonal orchard will start producing seed about 10 years after the initiation of the program although the genetic value of the seed is then still unknown. The orchard clone arrangement, however, prevents inbreeding. On this score the high-intensity program with its randomized orchard clones offers a simpler solution.

### Conclusions

The approach to the initiation of a black spruce selection program depends upon the particular situation of the organization, i.e. the funds, personnel, and facilities available, the seed supply and urgency to produce improved seed, the annual area to be regenerated, and the estimated genetic gains (which cannot be determined accurately at this time). Each of the two approaches discussed has certain advantages and disadvantages, but either one or the other may suit the needs of a particular organization. A better knowledge of heritability and genetic gains (based upon an adequate sample of populations and environments) would simplify the problem, but this cannot be obtained for some years.

## RED PINE

by

M.J. Holst

### Introduction

Red pine (*Pinus resinosa* Ait.) occurs mainly in the Great Lakes - St. Lawrence Forest Region and the Acadian Forest Region (Rowe 1972). Owing to its good stem form, uniform growth rate, and preference for sandy soils, it has been widely planted in Ontario and Quebec. Between 1900 and 1965, about 145,000 acres were planted to red pine in Canada (Cayford and Bickerstaff 1968).

Whether or not red pine lends itself to genetic improvement has been hotly debated. Fowler (1964a) mentioned that genetically it is the least variable of all the pine species studied to date; so selection of superior individuals or races may be unfruitful. Subsequently Fowler and Heimbürger (1969) estimated that genetic improvement of red pine will be difficult but by no means impossible. The expected improvement will be small compared with that in other coniferous species native to Canada, but even a modest improvement may be economically justifiable where red pine is extensively planted. Data from the Petawawa Forest Experiment Station (Holst 1975) suggest that plus-tree selection combined with testing of single-tree progenies is both feasible and effective.

### Population Structure

Throughout its range, red pine is exceptionally uniform in taxonomic as well as in morphological characteristics (Wright et al. 1963; Fowler 1964b). Its geographic variation has been studied in provenance tests and single-tree progeny tests in the Lake States since the early 1930's (Rudolf 1947) and in Canada since the early 1950's (Holst 1964, 1967). The problem is to determine how much genetic variation there is at the level of stands within regions and single-tree progenies within stands. The relative magnitude of variation will determine the approach to be taken in a plus-tree selection program.

In the Lake States, red pine provenances have shown only moderate variation in height - about 5 to 15% of the mean of the tests. This is small when compared with species with continent-wide ranges. Trees grown from seed collected in regions adjacent to a test site have on the average better survival and height than trees from distant regions. Within a region there is considerable stand-to-stand variation that can be utilized directly (Nienstaedt 1964, Rudolf 1964). The Canadian provenance tests show a similar magnitude of variation in height. The mean range of 10-year height was 92 to 110% of the experimental mean for one series of 10 experiments and 82 to 115% for another series with seven experiments. Thus much can be gained by using only the highly productive stands.

An indication of within-stand variation is obtained from single-tree progeny tests with randomly selected trees. The oldest study is one with 87 single-tree progenies from 14 regions in the Lake States. The trees were planted in 1931 and 1933 in northeastern Minnesota and were last measured in 1964 (Nienstaedt 1964). There were significant differences ( $P < .01$ ) among progenies in height, diameter, and survival. For the whole experiment the best progeny was 19% taller than the poorest. For trees from the regions adjacent to the planting site the range in height was only 8 to 9%. Thus the variation for distant regions is double that for adjacent regions. For diameter the best progeny exceeded the mean of the adjacent regions by 9%. Survival by progenies and regions was significantly different. The adjacent regions had 19 to 43% survival while the distant regions had only 10 to 23%. From a combined provenance and single-tree progeny test in Wisconsin, Lester and Barr (1965) concluded that within a region a 10% increase in height may be expected from seed collected in the better stands and that gains of the same magnitude may be expected from seed collected from the better individuals within a region.

The only Canadian single-tree progeny test comprises 10 trees from each of eight Petawawa stands in which 10-year height was measured. The stands were not significantly different, but the single-tree progenies were ( $P < .01$ ) and accounted for 21% of the variance (Holst 1975). The best progeny was 11% taller than the overall mean. In stands growing on fairly uniform and fertile red pine sites, and for which age was also determined accurately, there was a positive correlation between parent-tree height and progeny height ranging from  $r = .31$  to  $r = .61$ . Stands growing on rocky shallow soils showed both positive and negative correlation between parent-tree height and progeny height. The heritability ( $h^2$ ) for 10-year height was .31, which is within the range of height heritabilities (from .13 to .34) reported by Lester and Barr (1965).

### Choice of Traits

High-volume production of well-adapted, well-formed trees should be the aim of a tree-breeding effort in red pine. This goal can be reached through provenance and parent-tree selection, or a combination of the two.

Well-adapted trees can usually be selected within a site region (Hills 1959). Adaptation should be to both climate and soils and a considerable gain could be obtained by testing populations and single-tree progenies within a site region. The experience from the provenance tests planted within the red pine range in Canada is that certain provenances generally perform well in eastern Ontario, Quebec, and the Maritimes but poorly in southern Ontario and the Lake States. Other provenances perform poorly in all tests. In each location where a provenance experiment is planted there are some specific interactions depending mainly on climate. So to get well-adapted trees one should concentrate on the best local material and on those provenances that have proven themselves in provenance experiments within a specific site region.

The stem form of red pine is considered excellent, and it is hard to get specific data on scoring of stem form. Only Rudolf (1964) mentioned

vigor, form, and soundness. There were very few poor trees in the test planting, and the volume per acre calculated from the premium trees was only slightly smaller than the volume calculated from all trees. Nienstaedt (1964) noted some peculiar relations between heights and diameters. Some of the single-tree progenies were tall with small diameters while others were intermediate in height with large diameters. Thus it appears that stem form in red pine is generally good and does not lend itself to selection, while improvement in tree taper might be possible.

Heavy branches are considered undesirable. Selection for fine branches in isolated stands in northern Ontario has been successful (Fowler and Heimbürger 1969). Seed-production areas established in natural stands in the Lake States are being rogued to remove coarse-limbed trees. Perhaps an intensive search for trees with fine branches would turn up enough trees for further breeding.

### Strategy of Selection

Tree breeders have discussed whether an intensive search for plus trees would be worthwhile or whether the combined single-tree progeny-test and seed-orchard approach (testing 300 randomly selected trees as advocated by Wright [1964a, 1964b]) would be more efficient.

Selection of plus trees in red pine presents real difficulties. Most natural stands are of fire origin and are often descendants of a few old seed trees that survived earlier fires. Many a stand may therefore be considered a family of closely related individuals that looks very uniform - so uniform that any selection of plus trees seems out of the question.

With a methodical approach, however, it seems possible to solve the problem. First, stands within which selection is to be made should be located on sites typical of those normally planted to the species; one should also plan to make progeny tests on similar sites. These sites should be as uniform as possible in fertility. Second, by the method of comparison trees, the tallest trees within each family should be located (Holst 1975). Total height is measured and age determined by boring at breast height, or by counting whorls. Diameter is measured at breast height, and at half total height if one is interested in taper. Notes are made on branch size. A sample of five to seven of the tallest trees from a local stand should be adequate.

To facilitate progeny testing, the cones should be collected from the trees in good seed years, which may be 5 to 7 years apart. The cones open on the trees, and there is only a limited period in September-October in which cone collection can be made. To reduce the possibility of self-pollination, cones from isolated trees or small groups of trees should not be collected, and even in larger stands and plantations collection should only be made in certain portions of the crown (Fowler 1965b). In the controlled crosses produced by Fowler (1965a) and tested at Petawawa, it was found that in 9-year-old plants selfed progenies were 9% shorter than the local cross-pollinated controls (Holst and Fowler 1975). This inbreeding depression should be guarded against by collecting cones only from the

upper crowns of plus trees. A large stand suitable for plus-tree selection is shown in Fig. 10 and a plus tree in Fig. 11.

Scions from plus trees are best collected in the middle of winter and grafted on other rootstocks in a greenhouse. Outdoor grafting on saplings is also feasible. The rootstock should be red pine because red pine does not graft well on other pines. The successfully established ramets would then be planted into clonal orchards (or at least into clone banks), which would yield improved seed.

A typical program might prescribe selection of about 150 plus trees per site region, which would be chosen on the basis of growth rate, branch thickness, and taper. From such a selection one would reasonably expect a 10 to 15% increase in volume alone (Nienstaedt 1964; Lester 1964; Lester and Barr 1965). It has been shown that even increases of lesser magnitude in this species are economically justifiable (Lundgren and King 1965).

### Test Procedures

There are technical difficulties in testing a large number of progenies for small differences, such as the problem in finding large, uniform sites. Furthermore, red pine is very sensitive to site differences and seedbed density. In Michigan, Wright et al. (1963) found that 3-year-old seedlings in well-stocked portions of the seedbed (15 to 30 trees per square foot) were 31.5 cm tall whereas those in poorly stocked portions (two to five trees per square foot) averaged only 11.3 cm in height. In the nursery at the Petawawa Forest Experiment Station there has been the opposite trend. The effect on 4-year height of seedlings grown for 2 years in seedbeds of varying density and 2 years in a replicated nursery test was as follows: more than 100 seedlings per square foot, 46.6 cm; between 60 and 90 seedlings per square foot, 56.0 cm; and between 5 and 50 seedlings per square foot, 60.0 cm. One of the criticisms leveled against the old Lake State tests was that density in seedbeds was not recorded and that there were no replications of the sowings in the seedbeds (Fowler and Lester 1970).

Thus red pine progeny tests require experimental designs of great precision. The average weight per 1,000 seeds should be obtained. Sowings should be randomized and replicated and the sowing medium should be as uniform as possible. The same holds true for growing the transplants. Field tests should be planted on uniform sites in more than two locations. A randomized, complete-block design with few trees per plot and many replications is the most appropriate. In the single-tree progeny tests at Petawawa Forest Experiment Station 10 replications of the 10-tree plots were used. The Michigan test of 300 progenies was planted in five locations with 10 replications of four-tree plots, although the plan called for 15 replications and six-tree plots (Wright 1964a). If some of the test plantations are to be thinned to seedling seed orchards, plots should be small enough to leave only one tree per plot at the seed-production stage to avoid inbreeding because all trees of the same single-tree progeny are related through descent from the same mother. These problems of design for both progeny testing and seed production were discussed earlier in connection with seedling seed orchards.

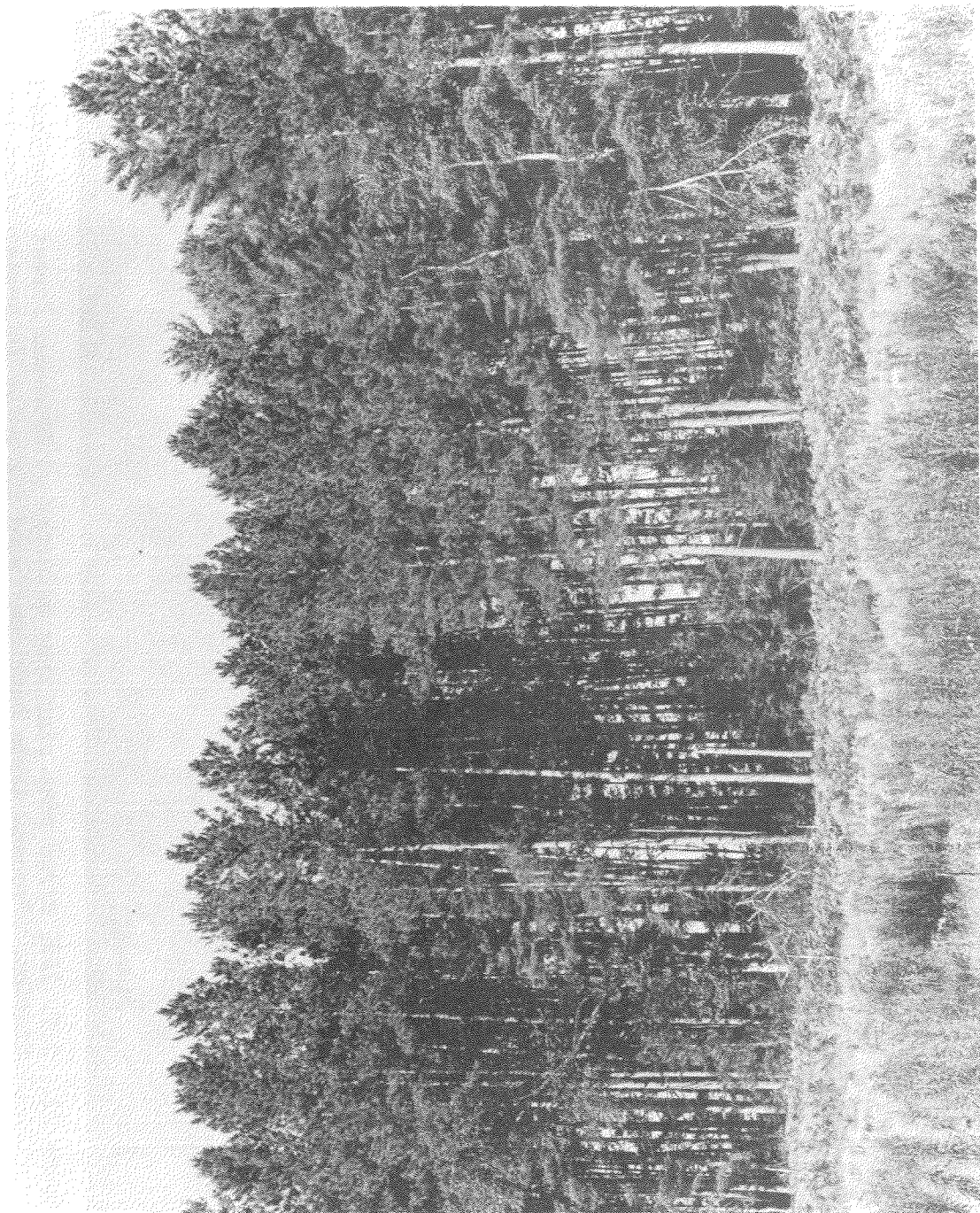


Figure 10. A large, closed stand of red pine at Petawawa suitable for plus-tree selection.



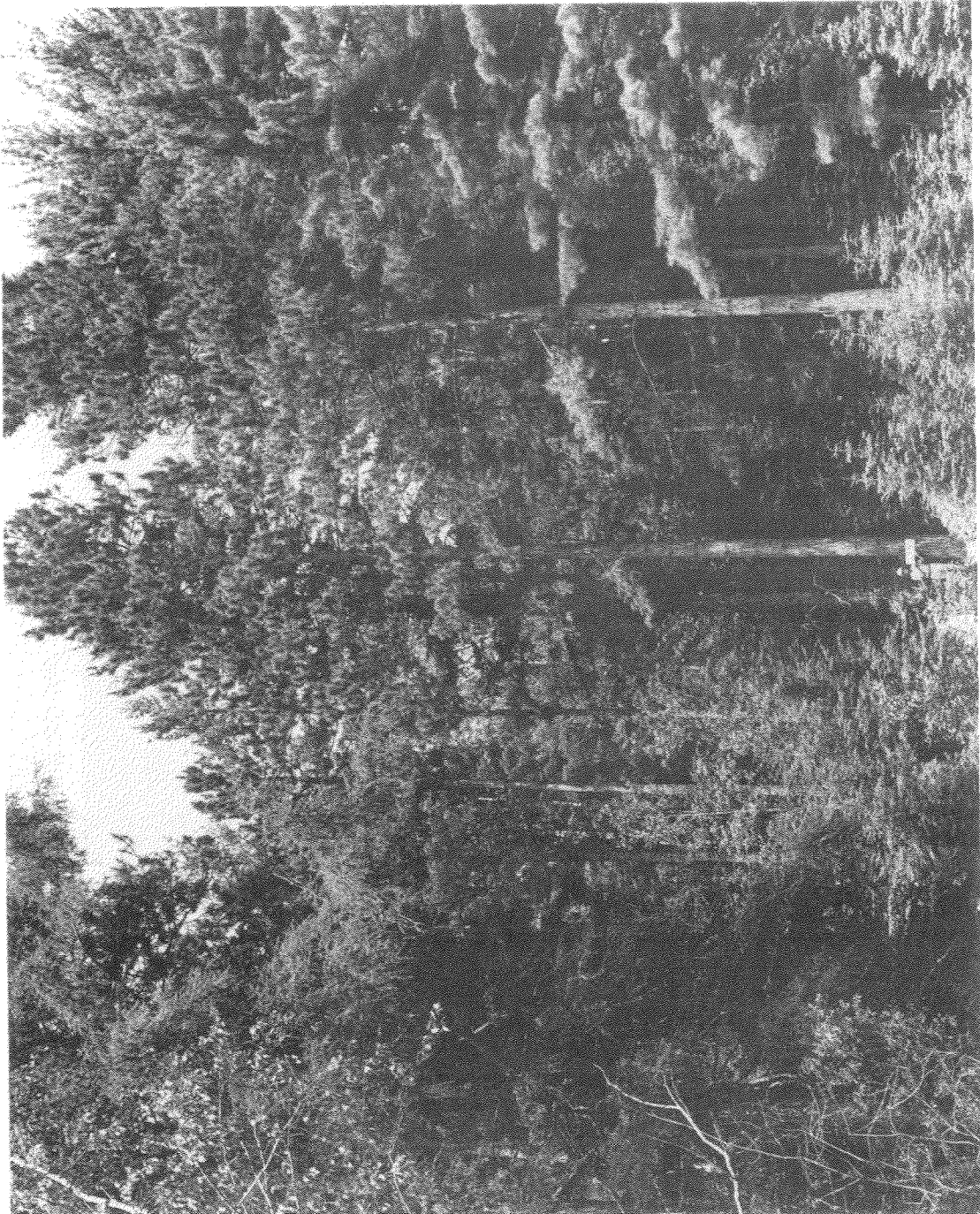


Figure 11. S.T. 150, a red pine plus tree selected at Petawawa Forest Experiment Station. Progeny tests have confirmed its value in transmitting the ability for fast height growth.

## Seed Production

In a combined progeny-test and seedling-seed-orchard scheme (Wright and Bull 1963), the tests can be measured at 15 or 20 years of age and the particular plantings designed for seedling orchards can then be thinned on the basis of the results. Alternatively, if the progeny tests serve the testing function only and grafted clonal orchards have been established for seed production, these orchards can be rogued on the basis of the progeny-test results.

Both seedlings and grafts of red pine start to produce cones when 15 to 20 years old. Female flowers are produced 3 to 4 years earlier than the male flowers. While the number of female flowers fluctuates from year to year in accordance with the climate, male flowers are produced in abundance every year on the most vigorous trees. Abundant female flower production is associated with high July temperatures in the previous year.

In an unfertilized orchard, good cone crops are produced at intervals of 3 to 7 years. Fertilization with ammonium nitrate and other cultural treatments have reduced the interval between crop years (Dyer 1970). Cone insects such as *Conophthorus resinosae* Hopk. and *Dioryctria disclusa* Heinr. may ruin cone crops in years of low production but tend to be relatively less destructive in years of high production (Lyons 1957). Cone crops are also influenced by spacing. In an 18-year-old plantation at Petawawa, Stiell (1971) found that trees spaced 4 x 4 feet to 21 x 21 feet produced 208 to 37,842 cones per acre. The attack of *Dioryctria disclusa* in a good cone crop year ranged from nil at 4 x 4 feet to 12% at 21 x 21 feet.

The total acreage of seed orchards required depends upon the average area to be regenerated annually. Using seed crop reports from the Lake States without fertilization, and a safety factor of 2, Rudolf (1959) estimated that 600 seed trees or 30 acres of seed-production area are needed to produce an average of 1 million plantable trees a year. A fertilized 7-acre seed-production area with 708 trees in southern Ontario produced 4.8 million viable seeds (perhaps 3 million plantable trees) in a medium crop year (Dyer 1970; Eng 1970), but the average annual production would be lower. Seed production in seedling seed orchards and grafted clonal orchards would be expected to be similar, and the figures cited could be used to plan seed production within broad limits.

## Conclusions

Red pine provenance experiments and single-tree progeny tests show only moderate variation in height and volume production. However, variation is sufficient to economically justify selection in areas where red pine is widely planted.

The plus trees are selected from the tallest trees in a stand. Within a site region a total of 150 trees should be selected. Cones should be collected for a combined single-tree progeny test and seed orchard. Scions may be collected for a grafted seed orchard.



As the magnitude of variation is rather small ( $\pm 10\%$  for height), great care is required in producing the plants for the tests. Seedbed media, nursery soil, and field-test sites should be as uniform as possible, and there should be adequate replication at each of the three levels of plant production.

The single-tree progeny tests should be planted in more than two locations and should be measured at 10, 15, and 20 years from seed, at which time the poor performers can be determined and cut. If a grafted seed orchard is made, the poor clones can be cut when the results of the single-tree progeny tests are in.

A conservative estimate of the expected gain in volume production from seed collected in the improved seed orchards is 10 to 15%.

# JACK PINE

by

C.W. Yeatman

## Introduction

Provenance tests have shown that growth of jack pine (*Pinus banksiana* Lamb., syn. *P. divaricata* [Ait.] Dumont) conforms to environmental gradients related to latitude (photoperiod) and length and temperature of the growing season (Schantz-Hansen and Jensen 1952; Rudolph 1964; Yeatman 1966; Canavera 1969). Provenance variation has also been shown in the incidence of pests (King 1971). Serious risk of reduced growth or survival attends the movement of seed beyond the limits of recognized ecological zones, e.g., Rowe's (1972) Forest Sections (Yeatman and Teich 1969). These constraints apply also to the breeding of jack pine, which must be pursued on a regional or district basis from selection and testing through to seed production and utilization (Klein 1968).

Early gains in productivity of as much as 10% over local sources can be expected if the best natural populations within an ecological zone are identified and used for seed collection (King 1973; Yeatman 1974). Establishment of stand tests in conjunction with controlled seed collection, production, and utilization is the first priority in a jack pine improvement program. Early and abundant production of closed (serotinous) cones ensures that repeated collections of seed can be made from selected stands by felling trees as required. Hence, for mass production of seed, immediate advantage can be taken of superior natural populations once their identity is known and provided the gene pool remains intact through natural regeneration or by restocking with plants or seed of local origin (Yeatman 1972). Plantation tests of stands will permit selection of the better seed sources as early as 10 years after the sowing of seed in a nursery.

Plus-tree selection is the first step toward improving the genetic quality in the better natural populations. As felling advances in a seed-production area, the area can be replanted with progenies of plus trees from the same population to create a seedling seed orchard. Improvements of stem straightness and crown form are particularly promising in jack pine in view of the variability within populations, high heritability, and impact of these characteristics on wood quality and yield. Increased growth and survival will also be sought. Action is needed now to develop the capacity to produce large quantities of well-adapted and improved jack pine seed required for expanding reforestation programs, and for direct seeding in particular (Cayford and Bickerstaff 1968; Scott 1970).

## Population Structure

Jack pine is most frequently distributed in the landscape as a mosaic of populations occupying specific habitats to which the species is

adapted. This is reflected in the large genetic differences found among populations from a single climatic zone (King 1966; King and Dawson 1971; Yeatman 1974).

Jack pine occurs on well-drained sites of low to moderate fertility and commonly grows in extensive, even-aged stands that reflect a fire origin. It is also found in mixture with hardwood and other coniferous species and is succeeded, in the absence of fire, by spruce-fir or pine mixtures on all but the driest sites (Cayford et al. 1967).

Gene exchange occurs readily by means of wind pollination, but greater opportunities for cross pollination exist among neighboring trees than among distant trees or between separate populations. Seed released from closed cones after fire is not widely dispersed from the parental trees. These factors, characteristic of natural regeneration of jack pine, tend to maintain neighborhoods of closely related trees and must be taken into account in searching for plus trees.

### Choice of Traits

Improvement is sought in survival, growth rate, fiber yield, and log quality of jack pine normally grown in even-aged, fully stocked stands. The ideal plus tree has the following phenotypic attributes, listed in order of importance.

#### 1. Absence of injurious diseases or insects.

A chronically diseased or infected tree is not a suitable candidate for breeding. Selection should be confined to healthy trees within healthy stands. This does not imply breeding for resistance, since a more realistic objective is to maintain an adaptive balance with indigenous disease and insect pests (Bingham et al. 1971).

#### 2. Straight, single stem.

Stem form is highly variable and generally poor, especially when jack pine grows in stands of moderate to low density, as is often the case with man-made forests. Examples of straight and crooked trees are shown in Fig. 12. Crown abrasion and competition for light are more uniform in a stand of straight trees than in one with many crooked and multistemmed trees. Trees with bent and crooked stems increase logging costs and yield logs of low recovery value for lumber (Dobie 1964). The high proportion of reaction wood formed in such stems reduces pulp yield and is a cause of weakness and warping in lumber (Jane 1956; Shelbourne 1969b).

#### 3. Wide branch angle.

Branch angle in jack pine varies greatly from tree to tree and is commonly less than 40 degrees with the stem (Fig. 13). Knot volume decreases with increasing branch angle, the result being higher pulp



Figure 12. Comparison of stem form in young jack pine. Plus tree, straight stem (left), vs. minus tree, crooked stem (right).

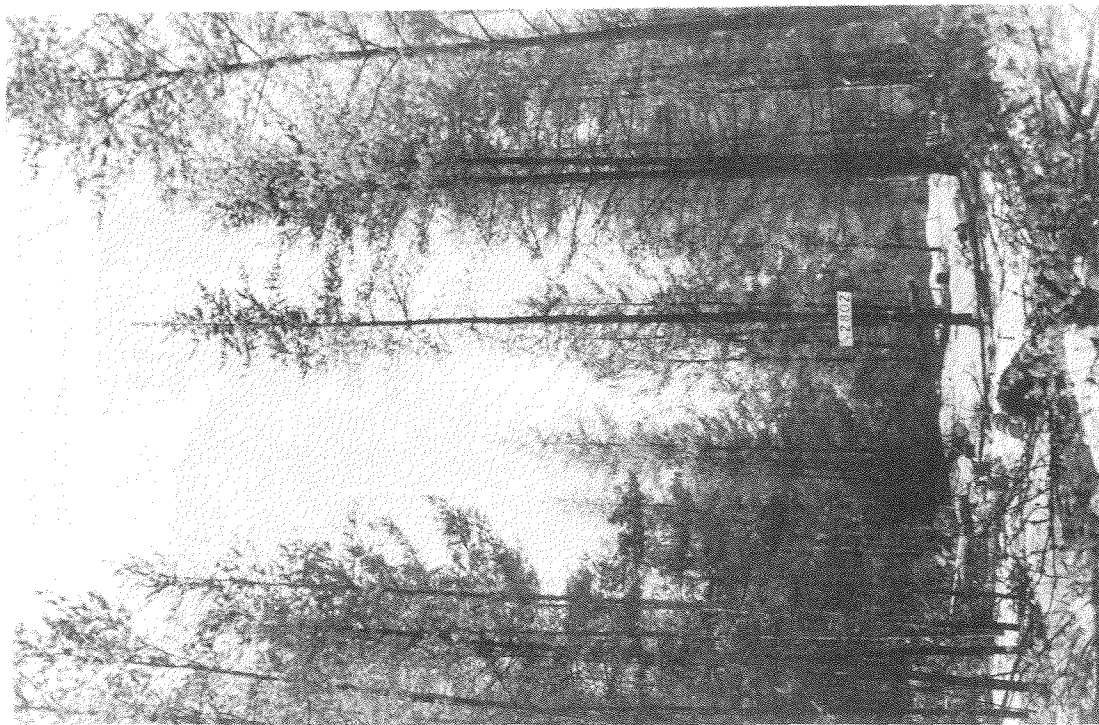


Figure 13. Comparison of branch angle between plus and minus trees in jack pine. Plus tree, wide angle (left), vs. minus tree, acute angle (right).

yields and increased lumber quality from trees with wide branch angle (Ehrenberg 1970). In a closed stand, a wide branch angle results in shorter and smaller branches (Woessner 1965) and a shorter length of branch occluded in the stem (in proportion to the sine of the angle).

#### 4. Uniform, multinodal branch habit.

Jack pine is multinodal (Shaw 1914); i.e. it sets two to three whorls of branches each year. Uniform branch development within and between whorls leads to a balanced crown, consistent knot size, and even stem taper and therefore to higher yield (Dyson 1969; Faulkner 1969). Late shoot development (lammas growth and prolepsis) in jack pine gives rise to short internodes and uneven branch development, and such trees of undesirable growth habit should be avoided in selection (Rudolph 1964).

#### 5. Above-average height and diameter.

Plus trees should be selected for above-average height and diameter within the dominant crown class. Vigor must be judged in each case in relation to stand history, the competitive position of the tree, and the growth of immediate neighbors. Phenotypic selection for characters strongly affected by competition is unreliable (Stern 1964), and progeny tests are needed to determine breeding values for vigor in jack pine.

#### 6. Closed cones.

Trees with closed (serotinous) cones predominate throughout much of the range of jack pine, but trees bearing open cones are found in most stands and are common in southern populations (Schoenike et al. 1959; Schoenike 1962). Closed cones are an asset for two reasons - economy of seed collection and insurance against fire. Seed can safely be stored in closed cones on the tree for several years and collected in quantity as required. In the event of fire, a preponderance of trees with closed cones ensures adequate natural regeneration (Roe 1963). Cone serotiny is highly heritable and appears to be governed by one or few genes (Rudolph et al. 1959; Teich 1970a; Sittmann and Tyson 1971).

#### 7. Straight cones.

Straight to slightly curved cones yield up to twice as many filled seeds per cone as do strongly curved cones (Schantz-Hansen 1941; Jeffers 1972). Efficiency of seed production in orchards is required to grow the large quantities of jack pine seed needed for direct seeding. Cone shape is highly heritable and easily recognized. Whenever possible, trees with strongly curved cones should be avoided as plus trees, although candidate plus trees should not be rejected on this criterion alone.

### Strategy of Selection

Adequate seed and vigorous scions are required from each plus tree if the objectives of seed production and improvement are to be met. Seed

is needed to establish seedling seed orchards and progeny tests, and grafts are required for clone tests and controlled breeding. Juvenile jack pine with small crowns bear insufficient seed, and mature trees have few vigorous branchlets suitable for grafting. The best opportunities for genetic expression and phenotypic selection, as well as for collection of seed and scions, are to be found in young to middle-aged stands of good site quality and with uniform, normal stocking of either pure or mixed species. Superior phenotypes tend to cluster in jack pine stands because of the family (nonrandom) structure of natural regeneration and localization of environmental effects. It is therefore necessary to select plus trees systematically according to a prescribed intensity - say one tree in 10 acres. At this rate 100 ten-acre blocks, or 1,000 acres of forest, would be surveyed to find 100 plus trees, a realistic goal for the establishment of a local breeding program, one of a number within a given ecological region.

Ocular selection is recommended for jack pine as the most efficient method of assembling breeding material in the first generation. Form characteristics are easily recognizable and rapid comparisons are possible among trees and among groups within a stand. Similarly, comparisons of height and diameter of select trees in relation to neighbors are readily made by eye. It is advisable to identify a number of candidate trees within an area being sampled before selecting the best among the candidates after a second look.

Plus-trees surveys are best made in the winter, when visibility is not impaired by the foliage of competing hardwood species. Dormant scions for grafting can be collected from January to March when, packed in snow and kept frozen, they can safely be transported and stored for long periods. Normally scions are grafted in a greenhouse during the latter part of winter, but spring grafting can be done under shelter in a nursery. Methods for rooting jack pine cuttings are being developed in Ontario (Dr. L. Zsuffa, personal communication).

Seed of trees with closed cones can be collected at any time of the year. However, climbing young to middle-aged jack pine grown in a closed canopy is hazardous and requires special tree ladders. There is little advantage to retaining the original tree in the forest as long as clonal propagation is assured. Felling is the more efficient way to gather seed and scions from the upper crown, and it also permits accurate measurement of height, taper, and branch angle.

### Test Procedures

Information to estimate breeding values is gained from both clones and progenies (families) of plus trees. Early comparisons among jack pine clones of traits of high heritability such as stem form and branch angle can be made in a breeding arboretum or clone bank. Simple replication, e.g. planting two rows of each clone in separate blocks, is necessary for statistical evaluation. On the evidence thus obtained the poorest genotypes can be rejected for breeding and their progenies culled from the



seedling seed orchards before substantial production of seed commences. To facilitate controlled breeding and observation, clone collections need to be planted on good jack pine sites that are protected from fire and easily accessible.

Progeny tests of jack pine can be conducted in two stages - by the initial use of open-pollinated seed from the plus trees, followed by the use of progenies from control pollination among clones. For comparison of growth and survival in different environments, tests need to be made at a number of locations representative of a range of sites in a region. The early tests based on open-pollinated seed will give first estimates of breeding values and will guide family selection in the seed orchard and choice of clones for controlled pollination (Wright and Bull 1963; Namkoong et al. 1966; Libby 1969b; Shelbourne 1969a; Burdon and Shelbourne 1971).

Pollinations on a practical scale can begin 6 to 8 years after grafting. The cones are mature after two further growing seasons. Pollinations may have to be repeated over several years to meet seed requirements for progeny tests and for planting in seedling seed orchards, priority being given the latter.

#### Seed Production

Because it has rapid juvenile growth and early seed production, jack pine is ideally suited to the use of seedling seed orchards, which, at least in the first generation of breeding, can most effectively be integrated with seed production areas and at minimum additional cost. Initially progenies from open pollination of locally selected plus trees will be planted to replace trees of the original stand cut for seed collection. Later planting will be done with progenies from controlled pollination. In this way early advantage can be taken of initial selections, progressive improvement being made in the seed orchard stock as poorer families and trees are culled from earlier plantings and better families are included in new plantings. Close spacing at planting, small family plots with many replications, and early and severe culling within and among families will result in relatively open stands of full-crowned trees.

Collection of cones may begin about age 5 years (Wright 1964b), and seed production can be expected to reach substantial quantities by 10 years of age. The background pollen of the surrounding population will ensure adequate filled seed in the first years of low pollen production, and the orchard seed will be true to type with respect to the genetic attributes of the population. Roe (1963) found that young plantations 9 to 13 years of age had accumulated as many viable seed per acre (ca. 470,000) as were found in unthinned 40-year-old stands or in overmature jack pine 70 to 80 years of age. The number of viable seed per acre stored in cones on the trees was about doubled for thinned stands of intermediate age.

In seedling seed orchards, cones can be collected economically from the ground for some years. By the time the cones are out of reach,



additional thinning on the basis of progeny-test results will further upgrade the genetic quality of the orchard. It can then be left to accumulate cones for some years before felling between 15 and 20 years of age for seed collection. By this time subsequent plantings of improved stock will be producing seed.

Regional seedling seed orchards combining the best populations and genotypes will be created when results are known from stand and progeny tests. To optimize the pollen background, such orchards may well be located in the vicinity of natural populations of superior genetic value. It cannot be expected that this stage will be reached until the tests have grown to about half-rotation age in, say, 20 to 30 years. In the meantime steady improvement in genetic quality will have been achieved within a broad genetic base while at the same time the required level of seed production will be maintained.

### Conclusions

Artificial regeneration of jack pine is necessary over extensive areas of boreal forest to restock natural stands after harvesting. Because of the magnitude of the task, errors in selection of seed source must be avoided and genetic improvement must be sought. Current information is sufficient for the former, and exploration and utilization of genetic variation between and within populations will achieve the latter. By integrating tree improvement with operational seed collection, costs will be minimized and effectiveness maximized. The immediate tasks are:

1. to select populations for current seed collection;
2. to create comparative tests of the seed collection areas in conjunction with normal reforestation programs;
3. to maintain the genetic quality of seed collection areas designated for future seed production and improvement;
4. to plan and initiate regional breeding programs based on plus-tree selection, creation of seedling seed orchards, and continued improvement through recurrent selection.

Plus-tree selection within the best populations and families, the development of improved seed-production areas, and the creation of pedigreed breeding populations will be the basis for the long-term improvement of jack pine in Canada.

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## ECOLOGICAL DESCRIPTION OF PETAWAWA FOREST EXPERIMENT STATION

### Location

The Station is in the Ottawa Valley between Ottawa and North Bay, Ontario. Station headquarters is at 46°00' north latitude and 77°26' west longitude. The area of the Station covers about 24,000 acres and is part of the Middle Ottawa Section of the Great Lakes - St. Lawrence Forest Region (Rowe 1972).

### Geology, Soils, and Natural Forests

The topography is flat to undulating. Elevation ranges from 370 feet (120 m) above sea level near the Ottawa River in the north to 950 feet (310 m) on the hilltops near the Petawawa River in the south. Precambrian gneisses underlie the entire area. During the Pleistocene Epoch the area was covered by glacial till and the lower levels were flooded by the northernmost extensions of the Champlain Sea. The soils are weakly developed podsoles.

Typical land types and their most common trees are: (1) dry delta sands and aeolian deposits with *Pinus banksiana* Lamb., *P. resinosa* Ait., *P. strobus* L., and *Populus tremuloides* Michx.; (2) fresh till plains and slopes with *Acer saccharum* Marsh., *Betula alleghaniensis* Britton, *Tsuga canadensis* (L.) Carr., and *Picea glauca* (Moench) Voss; (3) dry rocky hilltops with *Populus grandidentata* Michx., *Quercus rubra* L., and *Ostrya virginiana* (Mill.) K. Koch; and (4) moist to wet depressions with *Thuja occidentalis* L., *Larix laricina* (Du Roi) K. Koch, and *Picea mariana* (Mill.) B.S.P.

### Climate

General character: cool - temperate, continental. "B<sub>2</sub> Most Humid" in Thornthwaite classification (Hills 1959).

Mean annual precipitation: 31 inches (780 mm).

May-August precipitation: 11 inches (280 mm).

Mean July temperature: 78°F (25°C).

Mean January temperature: 18°F (-8°C).

Mean growing season (days above 42°F = 5.6°C): 178 days.

Mean frost-free season: 105 days.

## GLOSSARY

Some genetic and breeding terms used in this report are defined below. These were abbreviated from the *Glossary for Forest Tree Improvement Workers*, compiled by Dr. E.B. Snyder of the Southern Forest Experiment Station, U.S. Department of Agriculture (Snyder 1972), or taken from textbooks on breeding, genetics, and forest genetics (Allard 1960; Crow 1966; Falconer 1960; Sinnott et al. 1958; Wright 1962).

- Allele:* One of a pair or series of genes located in the same position on a given chromosome and affecting the same trait. In a single diploid organism, only one allele pair is present, but in a population a larger number is possible (multiple alleles).
- Breeding:* The theory and practice of systematic genetic improvement of a species.
- Breeding value:* The value of an individual, judged by the mean value of its progeny.
- Clone:* A group of genetically identical plants derived from a single individual (ortet) by vegetative propagation.
- Combining ability:* The relative ability of a genotype to transmit genes for desirable performance. "Good *general* combining ability of a parent" indicates the high average performance of its progeny from crosses with many parents; "good *specific* combining ability" refers to the above-average performance of its progeny from certain parental combinations.
- Diploid:* Refers to the somatic or zygotic chromosome number in the nucleus of the cell. A cell is diploid when it contains two sets of chromosomes ( $2n$ ), one set from each parent. Most higher organisms are diploid, their sex cells *haploid* ( $n$ ).
- Gene:* The smallest transmissible unit of genetic material consistently associated with a primary genetic effect. The genes are ultramicroscopic and act as if linearly arranged at fixed places (loci) on a chromosome. Each gene governs a certain physiological effect in a cell and interacts with other genes and the environment.
- Genetics:* The science dealing with the causes of variation among plants or animals related by descent.
- Genetic correlation:* A measure of the degree of genetic relationship between two characters in the same population, calculated from groups of related individuals such as progenies from open or controlled pollination. (Not to be confused with phenotypic correlation.)

*Genetic processes:* These include: *mutation* - the sudden appearance of new gene alleles; *selection* - the differential perpetuation of genes from one generation to the next as a result of unequal reproduction and survival; *random genetic drift* - the accidental fluctuation in gene frequencies from generation to generation in small populations; and *migration* - the interchange of genes with neighboring populations.

*Genotype:* An individual's hereditary constitution.

*Genotype-environment interaction:* The failure of members of a population to maintain the same relative ranks or levels of performance in different environments.

*Half-sib family:* A group of individuals related by descent from one common parent, as the seedlings from the same open-pollinated mother tree. A family of *full-sibs* has both parents in common.

*Heritability:* The degree to which a character is influenced by heredity as compared with influence by the environment, calculated from the ratio of variance or from a parent-progeny regression. *Narrow-sense heritability* is the percentage of additive genetic variance in phenotypic variance and is obtained from progeny tests based on open or controlled pollination; *broad-sense heritability* is the percentage of total genetic variance (additive and nonadditive) in phenotypic variance and is obtained from clone tests.

*Inbreeding:* The breeding of individuals more closely related than mates chosen at random from the population. Its most extreme form is selfing.

*Linkage:* The joint transmission of several inherited characters from parent to progeny when genes controlling these characters are situated next to each other on the same chromosome.

*Mass selection:* A number of suitable individuals are selected from a larger population (such as wild stands) to reconstitute a new breeding population.

*Mating design (system):* The pattern of cross-pollinations set up between individuals, usually in preparation for progeny testing.

*Ortet:* The original plant from which a clone has been derived.

*Phenotype:* The organism or character as we see it; the result of the interaction of genes (genotype) with the environment.

*Pleiotropism:* Applies to the situation in which a single gene influences several characters that are not obviously related. This is in contrast to the effect of minor genes (where a character is controlled by many genes).



- Pollination:* The deposition of pollen on the receptive part of the female flower. *Open* pollination refers to natural pollination by wind or insects, in which only the female parent is known and from which estimates of general combining ability can be obtained. *Controlled* pollination involves the isolation of the female flower and pollination from a known male parent and leads to estimates of both general and specific combining ability.
- Population:* Genetically, a community of interbreeding individuals.
- Population structure:* The genetic constitution of a population as described by its array of gene frequencies. Population structure is determined by population size, the genetic processes that act within it (mutation, selection, genetic drift, migration), and the mating system (inbreeding or outbreeding). Gene frequencies are estimated from the distribution of phenotypic classes in the material under observation.
- Progeny test:* Evaluation of the parents by comparing the performance of their offspring.
- Provenance:* From the Latin *provenire* (to come forth); the source or place of origin of pollen, seed, or vegetative material.
- Ramet:* An individual member of a clone such as a graft or cutting derived from the same ortet.
- Seed orchard:* An orchard established with clones or seedlings from selected trees, isolated to reduce pollination from outside sources, and cultured for early and abundant production of seed.
- Seed-production area:* A plus stand (natural or planted) that is upgraded by removal of undesirable trees and cultured to increase seed production.
- Selection:* Often synonymous with "artificial selection," namely the activity of the breeder in choosing individuals from a larger population. Natural selection is one of the genetic processes that determine evolution.
- Selection differential:* The difference between the mean of the whole population and the mean of the selected group.
- Selection intensity:* The proportion or percentage of selected individuals used in the calculation of genetic gain.
- Vegetative propagation:* Propagation of a plant by asexual means, as in budding, dividing, grafting, rooting, and air layering.